

The modelling of past land cover

A Swiss case study

Welmoed Soepboer

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The modelling of past land cover

A Swiss case study

Het modelleren van landoppervlakbedekking in het verleden

Zwitserland nader bekeken

(met een samenvatting in het Nederlands)

Proefschrift

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.. universities are truly storehouses of knowledge: students arrive from school confident that they know very nearly everything, and they leave years later certain that they know practically nothing. Where did the knowledge go in the meantime? Into the university, of course, where it is carefully dried and stored.

Terry Pratchett, Ian Stewart & Jack Cohen
The science of discworld

For the restless...

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CHAPTER 1

GENERAL INTRODUCTION, SYNOPSIS AND CONCLUSIONS

Introduction

Modelling land cover in the past is dealing with the biophysical state of the earth's surface and its immediate subsurface. Forests, grasslands, and wetlands are examples of land cover. Land cover is nowadays mainly influenced by land use, which is defined by the manipulation and purpose for which the land is used (e.g., logging, ranching, and agriculture). Land cover and land use are influenced by climatic, biophysical, and socio-economic factors (Turner II *et al.*, 1995). In return, however, climatic variability is affected by changes in soil moisture, evapotranspiration, and albedo (Fuller and Ottke, 2002). These biophysical factors are directly linked to land cover change.

Presently, the earth system faces ecological changes like desertification, freshwater decline, and biodiversity loss. Furthermore, there is debate about the causes and consequences of the current global warming (IPCC, 2007). It has been suggested that the influence of man on climate began already with the onset of agriculture, 8000 years ago (Ruddiman, 2003; Ruddiman, 2005). In such circumstances, it is paramount to study the earth system in the past to establish baseline conditions, to examine the timing and dynamics of natural variability in climate, ocean circulation, or land cover. In addition, to better understand the interacting processes that give rise to the variability in the system. In this way, the understanding of the system, as well as the knowledge of the followed pathway, will provide necessary information about the present state and the anticipated future global environmental change. The complexity of global environmental change also requires the understanding of land cover and land use change in the past.

Assessing land cover change in the past in the absence of written documents or remote sensing data is commonly done by pollen analysis. Already in the 1910s von Post realized (Davis, 2000) that the analysis of fossil pollen from peat or lake deposits could provide a measure of vegetation composition at the time of pollen deposition, e.g., as a sort of remotely sensed image (Prentice, 1988). In every growing season lakes, mires, or moss polsters record and store the composition and amount of pollen released by the surrounding vegetation (see Figure 1).

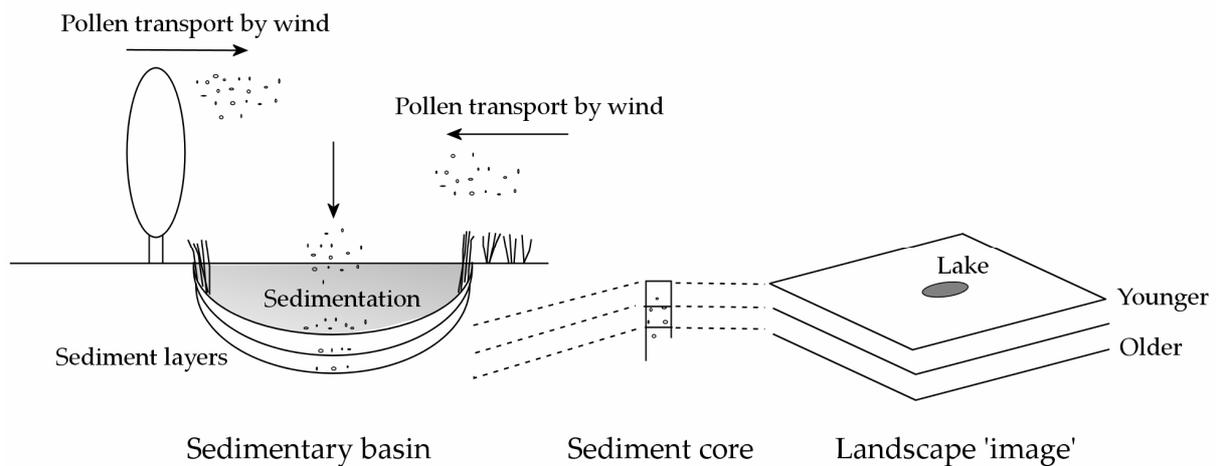


Figure 1 Pollen is produced by vegetation and amongst others transported by wind above the canopy. Pollen that falls out above a lake will be deposited on surface of the lake and ultimately settle in the lake sediment. Over the years continuous and multiple sediment layers build up. Once the sediment is cored and the pollen extracted and analysed, the pollen assemblages allow reconstruction of past vegetation and theories about past landscapes arise, much like remote sensing images

Analyzing the pollen samples from sediment cores allows studying vegetation change over time-spans of 10^{-1} to 10^6 years (e.g., Berglund *et al.*, 1996; Birks, 2005).

However, the relationship between pollen and vegetation is not as straightforward as initially thought. There are several dispersal mechanisms from the pollen source to the depositional basin, e.g. through wind in the trunk space, through wind over the canopy, through rain-out, through river water or side wash, or through redeposition and mixing processes in the basin (Tauber, 1965; Prentice, 1988). Differential pollen productivity of plant species and differential dispersal and preservation of pollen grains may lead to a bias in representation or even the absence of certain plants in the pollen record (Prentice, 1988; Jackson, 1994). In addition, despite continuous improvements in palynology (Punt *et al.*, 2003; Beug, 2004) it is often difficult or sometimes impossible to identify pollen to species or even genus level. Plants closer to a depositional basin will contribute more to the pollen record than plants further away. Thus, also the basin size will influence the composition of a pollen sample: in larger basins the influence of regional vegetation is larger than the amount of pollen originating from local vegetation (Andersen, 1970; Janssen, 1973; Jacobson and Bradshaw, 1981; Prentice, 1988; Sugita, 1994). Also, the pollen productivity per species may not be constant between regions (Calcote, 1995).

Several attempts have been made to calibrate the pollen-vegetation relationship. POLLANDCAL (POLLen-LANDscape CALibration) is an international network of palynologists who aim to develop and improve methods to infer quantitative vegetation and landscape characteristics at various spatial scales. This is done for the purpose of nature conservancy and landscape management (at local scale), and global environmental change research (at regional to global scale). Within the POLLANDCAL network the main objective is to develop

further a calibration model for the (modern) pollen-vegetation relationship, called the Extended R-Value model (Parsons and Prentice, 1981; Prentice and Parsons, 1983; Sugita, 1993). However, also the Prentice-Sugita model that deals with pollen dispersal and deposition is used (Prentice, 1985, 1988; Sugita, 1994; Sugita *et al.*, 1999). With these models, amongst others, Pollen Productivity Estimates (PPE) can be calculated that can subsequently be used for hypothesis testing of vegetation theories as well as for quantitative reconstruction of past vegetation.

The present study is a contribution to the POLLANDCAL network. The specific aim of this thesis is to improve the interpretation of pollen diagrams by analysing modern-vegetation relationships. Subsequently, we use the parameters of the pollen-vegetation relationship for hypothesis testing and the reconstruction of past vegetation at a regional scale. The research was carried out using pollen and vegetation data from Switzerland.

Towards the Extended R-value model

The quantitative calibration of pollen and the vegetation that produced it started almost 50 years ago. There were two ways in how the modelling of the pollen-vegetation relationship was improved. The first step concentrated on the calibration of the relationship itself, leading to the development of the Extended R-value models (ERV-models). The second step improved the way vegetation abundance was included, by modelling pollen dispersal and deposition (Prentice-Sugita model).

Davis (1963) introduced a simple correction factor (R-value) to transform pollen percentages of certain taxa into vegetation abundance percentages within a certain distance Z from the centre of a sedimentary basin. The R-value is defined as follows:

$$r_i = \frac{p_{i,k}}{v_{i,k}} \quad (1),$$

where $p_{i,k}$ is the pollen percentage of taxon i in the pollen assemblage at site k , and $v_{i,k}$ is the vegetation percentage of taxon i in the surrounding vegetation of the specified area. In theory and in practise, the R-value expressed over- or underrepresentation of the pollen taxa in pollen diagrams per site. The R-values vary substantially between sites because they depend on the species composition in the vegetation (Davis, 1963; Andersen, 1970). However, the relative R-values (ratio of the R-value of a species to the R-value of a reference species) are constant when no pollen is added from outside Z . This assumption only holds for sites in areas with very homogeneous vegetation over large distances.

Therefore, Andersen (1970) suggested a linear model that also included a background pollen component from vegetation outside Z , that does not need to be homogenous. Instead of percentage cover of vegetation, he used the crown area and basal area of the forests in Denmark. He also used semi-absolute pollen data, namely relative tree pollen deposition. This model can be described as:

$$y_{i,k} = \alpha_i \cdot x_{i,k} + \omega_i \quad (2),$$

where $y_{i,k}$ is the pollen loading of taxon i at site k , defined as the pollen input on the surface of a basin [number of pollen grains for total pollen loading or grains m^{-2} for mean pollen loading], α_i is a pollen representation factor of species i [e.g., grains $\text{m}^2 \text{kg}^{-1}$ or number of grains], $x_{i,k}$ is the vegetation abundance of species i at site k within distance Z [e.g., in kg m^{-2} or $\text{m}^2 \text{m}^{-2}$], and ω_i is the portion of pollen loading of species i produced by vegetation beyond distance Z [number of grains or grains m^{-2}] (Andersen, 1970; Parsons and Prentice, 1981; Prentice and Parsons, 1983; Prentice and Webb III, 1986; Sugita, 1994).

For lakes, the quantification of the pollen-vegetation relationships depends on absolute pollen deposition data, such as pollen accumulation rates (PAR, [grains $\text{cm}^{-2} \text{yr}^{-1}$]). However, to calculate PAR, information on the sedimentation rate or deposition time is needed. Moreover, PAR may vary considerably, both within and between lakes (Davis and Brubaker, 1973; Davis, 2000), whereas pollen percentages are more stable. Nevertheless, the interdependence of pollen percentages hinders quantification of pollen-vegetation relationships, because non-linearity (the “Fagerlind effect”) can occur in the pollen-vegetation relationship (Fagerlind, 1952; Davis, 1963; Parsons and Prentice, 1981; Prentice and Parsons, 1983; Prentice and Webb III, 1986; Jackson, 1994). Equation 2 can only hold as a first approximation for proportional data when no dominant species is present in the vegetation and pollen productivity is not too variable between species (Prentice, 1988).

Parsons and Prentice (1981) and Prentice and Parsons (1983) defined a calibration model to use with proportional data: the extended R-value model. Here, the original R-value model by Davis (1963) was extended with a background pollen component. Currently, three ERV sub-models exist, each with different assumptions about the background component. A site factor (f_k) is necessary to relate pollen percentages to vegetation percentages, considering the assumptions and definitions of the background terms specified for the sub-models.

Two parameters for each taxon in the ERV sub-models (i.e., the pollen representation factor and the background component) are estimated for all taxa by a maximum likelihood function, assuming a multinomial distribution for pollen percentages. The goodness-of-fit between the model and pollen and vegetation data is assessed by changes in the likelihood function score. In theory, the likelihood function scores decrease and approach an asymptote as the area of vegetation data (or the radius of the area) increases (Sugita, 1994).

For sub-model 1 it is assumed that the background pollen percentage is constant for each taxon. Therefore, the background pollen loading for each taxon (ω_i) is a constant proportion of the total pollen loading ($y_{\bullet,k}$) at site k :

$$\omega_i = z_i \cdot y_{\bullet,k} \quad (3),$$

where z_i is the background pollen percentage. The site factor for sub-model 1 then becomes (Prentice, 1988):

$$f_k \equiv \frac{1 - \sum_{j=1}^l z_j}{\sum_{j=1}^l \alpha_j \cdot v_{j,k}} \quad (4),$$

where $j=1$ to l includes all species. Sub-model 1 becomes:

$$p_{i,k} = \alpha_i \cdot v_{i,k} \cdot f_k + z_i \quad (5).$$

In equation 5, ' $v_{i,k} \cdot f_k$ ' ('adjusted vegetation proportion') is linearly related to $p_{i,k}$ (Parsons and Prentice, 1981; Prentice and Webb III, 1986; Sugita *et al.*, 1999).

For sub-model 2 it is assumed that the constant background pollen term of taxon i (z_i) is the ratio of the pollen loading of that taxon to the total plant abundance (of all taxa involved), within the area the vegetation abundance is compared with pollen data. This means that both the background pollen loading for each taxon and the total plant abundance ($\varphi_{\bullet k}$) are assumed constant regardless of sampling sites:

$$\omega_i = z_i \cdot \varphi_{\bullet k} \quad (6).$$

The site factor for sub-model 2 is:

$$f_k \equiv \sum_{j=1}^l \alpha_j \cdot v_{j,k} + z_j \quad (7).$$

And sub-model 2 subsequently becomes:

$$p_{ik} \cdot f_k = \alpha_i \cdot v_{i,k} + z_i \quad (8).$$

' $p_{i,k} \cdot f_k$ ' (the 'adjusted pollen proportion') is linearly related to $v_{i,k}$ (Parsons and Prentice, 1981; Prentice and Parsons, 1983; Sugita *et al.*, 1999).

Sugita (1994) proposed ERV sub-model 3. This sub-model uses pollen percentages and absolute vegetation measurement units (kg m^{-2} or $\text{m}^2 \text{m}^{-2}$) and assumes constant background pollen loading among sites. The site factor for sub-model 3 then becomes:

$$f_k \equiv \sum_{j=1}^l \alpha_j \cdot x_{j,k} + \omega_j \quad (9).$$

Therefore, sub-model 3 becomes:

$$p_{i,k} \cdot f_k = \alpha_i \cdot x_{i,k} + \omega_i \quad (10).$$

' $p_{i,k} \cdot f_k$ ' (the 'adjusted pollen proportion' or relative pollen loading) is linearly related to $x_{i,k}$.

Towards the Prentice-Sugita Model

Before pollen is calibrated to represent vegetation, also the “pollen’s view of the landscape” should be taken into account (Prentice and Webb III, 1986). Pollen grains are released by plants into the atmosphere. Some will be deposited nearby, but others will be transported further away. The number of pollen grains that remains airborne declines with increasing distance from the source plant. This decline can be modelled by using an atmospheric deposition model (Sutton, 1953) that describes how particles are emitted by a ground level source (Tauber, 1965; Prentice, 1985). The ground level is appropriate (Prentice, 1985) under the assumption that most pollen are released from a forest canopy (a more or less level surface) and deposited at a single point, e.g., the centre of a lake or bog (Prentice, 1985). The proportion of pollen of species i deposited at a distance z relative to the total pollen released at the source, $g_i(z)$, then becomes:

$$g_i(z) = b_i \cdot \gamma \cdot z^{\gamma-1} \cdot e^{-b_i \cdot z^\gamma} \quad (11),$$

where b_i [dimensionless] in neutral atmospheric conditions is defined as $75.2 \cdot v_g \cdot u^{-1}$, where v_g is the velocity of deposition of the pollen grains [m s^{-1}] and u the average wind speed [m s^{-1}]. The velocity of deposition is assumed equivalent to the terminal velocity of fall speed of the pollen grains (Prentice, 1985). The value for b_i depends, therefore, on pollen grain characteristics that are species-dependent. The value of γ is approximately 0.125 (Prentice, 1985, 1988; Sugita, 1994). In unstable atmospheric conditions the multiplier in the equation for b_i can be 54 or 32 (Jackson and Lyford, 1999).

The pollen deposition of species i coming from within a certain distance z becomes at a point in the centre of a circular basin (like a bog or moss polster):

$$y_{i,k} = P_i \cdot \int_R^z \overline{x_{i,k}}(z) \cdot g_i(z) \cdot dz \quad (12),$$

where P_i is the absolute pollen productivity, R is the radius of the basin [m], $\overline{x_{i,k}}(z)$ is the mean plant abundance of species i at distance z from the centre of the basin [basal area m^2 , kg m^{-2} , etc.].

Sugita (1993) created a model of pollen deposition for an entire lake surface, where pollen is homogenized in the water column before settling onto the lake bottom (Davis and Brubaker, 1973). The Sugita model for total pollen loading on a circular lake surface coming from within distance z is:

$$y_{i,k} = \int_R^z \frac{\pi \cdot R \cdot P_i \cdot \overline{x_{i,k}}(z)}{2} \cdot \left[\int_{z-R}^{z+R} g_i(x) \cdot dx \right] \cdot dz \quad (13).$$

The basic assumptions of the Prentice-Sugita model are:

- the basin is a circular opening in the canopy;
- pollen dispersal is even in all directions;
- the only drivers of pollen transport are wind above the canopy and gravity beneath it;
- pollen productivity is constant per taxon;
- the spatial distribution of each taxon is given as a function of distance from the centre of the basin;
- pollen deposition from a source plant is approximated by a two-dimensional function derived from Sutton's (1953) model for diffusion of small particles from a source at ground level;
- for the Sugita model it is assumed that all pollen deposited on the sampling basin are homogenized before sedimentation.

Equations 12 and 13 are isomorphic to equation 2 by dividing the integral into a part over R to Z (within the source area) and a part from Z to z (outside the source area). In effect, the Prentice-Sugita model is a distance-weighting model that gives higher weight to vegetation closer to the basin and down weights vegetation further away. Several other methods have been proposed to weigh the plant abundance in relation to the distance from the basin, for instance, by stepwise inverse weighting of the distance or stepwise inverse squared-distance (Calcote, 1995; Jackson and Kearsley, 1998). The Prentice-Sugita model is theoretically the most adequate method to distance-weight vegetation, because it is species-specific, it considers pollen grain characteristics. Only then the biases between taxa in pollen assemblages, caused by pollen productivity and dispersal, are separated and assessed (Sugita, 1994). If the Prentice-Sugita model is used to distance-weight the available vegetation abundance data, the ERV sub-models produce two parameters per stepwise increasing distance from the basin: a pollen productivity estimate (PPE or $\hat{\alpha}_i$) and a background pollen component (ω_i).

Relevant Source Area of Pollen

Janssen (1973) discriminated local from regional pollen deposition based on the decline in pollen deposition with increasing distance from the source plant. He distinguished four kinds of pollen deposition with increasing distance from the source vegetation:

- local;
- extra-local (ca. 100 m from the source);
- regional (similar within a region with the same large vegetation type);
- extra-regional (from outside the region).

Prentice (1985) translated these terms for basins; local being vegetation within 20 m from the edge, extra-local from 20 m to 200 m, regional from 2 to 200 km and extra-regional beyond 200 km. However, these are qualitative descriptions of the pollen source area. Prentice (1985) also defined a more quantitative description based on the Prentice model, called the 70% pollen source area. The 70% radius is a function of basin size and species-specific parameter b_i . For instance, for *Quercus* he found for a 70% source area of 55 m and 34 km, respectively, for basins with a radius of 0 m and 300 m.

Sugita (1994) elaborated the definition of pollen source area, because he found that much shorter distances were sufficient to provide optimum correlations between pollen and plant abundance. He defined a Relevant Source Area of Pollen (RSAP) out to the distance from the sedimentary basin where the relationship between pollen and (distance-weighted) vegetation abundance does not improve by considering more vegetation data from further away (Sugita, 1994). For his simulations about 30-45% of the total pollen loading came from within the RSAP. The vegetation inside the RSAP is the source for the local pollen loading component (combining local and extra-local in one term), while the vegetation outside the RSAP produces the regional pollen loading component (or background pollen component). The extra-regional component is smaller than 5-10% and may therefore be neglected (Sugita, 2007a). The local pollen loading corresponds to variations in the local abundance of vegetation, whereas regional pollen is uniform from basin to basin.

The RSAP depends mostly on basin size and vegetation heterogeneity. The RSAP of moss polsters and forest hollows is between 50 and 400 m (Sugita, 1994; Calcote, 1995; Broström *et al.*, 2005; Bunting *et al.*, 2005). For lakes RSAP between 600 to 1700 m have been found (Sugita, 1994; Sugita *et al.*, 1999; Nielsen and Sugita, 2005). For basins of a given size and under fixed atmospheric conditions, vegetation patch size and spatial resolution of the vegetation survey are the two most important parameters influencing RSAP (Bunting *et al.*, 2004).

Estimating the composition of past vegetation

The inverse forms of the ERV sub-models could potentially be used to reconstruct past vegetation, if fossil pollen and PPE are available (Prentice, 1988). While PPE might be considered constant through time as a first approximation, the background pollen component depends directly on regional vegetation that is influenced by climate, plant migration, biophysical factors, and human impact (Sugita, 2007b). Therefore, Sugita (2007a; 2007b) introduced the Landscape Reconstruction Algorithm (LRA) that is applicable for regions where PPE are available. The LRA consists of two sub-models, REVEALS and LOVE, each suitable for a different spatial scale. REVEALS (Regional Estimates of VEgetation Abundance at Large Sites) allows reconstructing quantitatively regional vegetation composition from fossil pollen records collected from large lakes (Sugita, 2007a). LOVE (LOcal VEgetation Estimates) allows estimating local vegetation abundance using regional vegetation estimates from REVEALS and pollen assemblages from small lakes of various sizes (Sugita, 2007b).

The equation used for estimating the proportional regional vegetation composition (\hat{V}_i) of taxon i is:

$$\hat{V}_i = \frac{n_{i,k} / \hat{\alpha}_i K_i}{\sum_{j=1}^m (n_{j,k} / \hat{\alpha}_j K_j)} \quad (14),$$

where t is the number of plant taxa used for reconstruction, $n_{i,k}$ is the pollen count of taxon i at site k , $\hat{\alpha}_i$ is the relative pollen productivity estimate of taxon i and K_i is the “pollen dis-

persal-deposition coefficient" of species i , defined as $\int_R^{Z_{\max}} g_i(z) \cdot dz$. In the definition of K_i , R represents radius of a large lake [m] from which pollen samples are collected, Z_{\max} a radius within which >90% of pollen comes from [m].

Used Models and Software

In this thesis most of the afore-mentioned models have been applied, such as the ERV sub-models and the Prentice-Sugita model. Within the POLLANDCAL network the models have been incorporated in different software. For clarity, a list of software is provided below.

ERV-model

The ERV sub-models are used to calculate Pollen Representation Factors or Pollen Productivity Estimates, depending on the type of distance-weighting. In Chapter 2 of this thesis ERV6 (Sugita, unpublished software) is used. It is a model in which calibration and distance-weighting approaches are combined. It allows modelling with three ERV sub-models as well as four different methods to distance-weight vegetation abundance. For Chapter 5 an adapted version has been used, that is similar to ERV6, but which allows also variance and covariance estimation.

POLLSCAPE

POLLSCAPE (Sugita, 2006) is a modelling scheme that uses vegetation and landscape maps to generate pollen loading and assemblages in sedimentary basins (lakes or mires). It uses the Prentice-Sugita model with several parameters (e.g., fall speed of pollen, wind speed, pollen productivity estimates, basin size, etc.). POLSIM is the software that includes POLLSCAPE. This program uses the Ring-Source model (Sugita *et al.*, 1999) as is used in ERV6. There is also a cell-based program suite with almost the same functions, called HUMPOL (Bunting and Middleton, 2005). In this thesis most programs were used from the former software suite. POLLSCAPE was used for the studies described in Chapter 3 and 4. When POLLSCAPE is mentioned, the programs underneath are often also used:

- OPENLAND (Eklöf *et al.*, 2004) is software used to calculate distance-weighted plant abundance from a digitised vegetation or land cover map by placing concentric rings around the sedimentation basin and calculating the mean vegetation abundance per distance class. The vegetation composition can represent real landscapes or may be created by using MOSAIC (Middleton and Bunting, 2004).
- In MOSAIC (Middleton and Bunting, 2004) a simulated landscape can be created with different patterns and different taxon percentages per land cover. This software is usually used to test hypotheses concerning vegetation patterns and spatial scale.

LRA

The LRA is a tool to reconstruct past vegetation. REVEALS is used for the pollen records collected from large lakes (Sugita, 2007a). LOVE estimates local vegetation abundance using regional vegetation estimates from REVEALS and pollen assemblages from small lakes of various sizes (Sugita, 2007b). REVEALS was used for the study described in Chapter 5.

Study area

Switzerland is relatively small country in Central Europe. It can roughly be divided into three geographical regions: the Jura Mountains, the Swiss Plateau, and the Alps. Each region is characterised by a difference in elevation and undulation. The Swiss Plateau is the flattest area and is situated below 800 m above sea level (asl). The Jura Mountains are higher, up to 1500 m asl. The Alps are much higher, with mountain peaks over 4000 m asl, but also with some lower, incised valleys.

The soil parent material in Switzerland is of glacial, fluvio-glacial and lacustrine origin. Also, rock outcrops occur. On the Swiss Plateau very productive to productive soils are found, characterised by good drainage and fertility. These conditions have allowed this part of Switzerland to be populated since the Mesolithic (Tinner *et al.*, 2007). The climate in Switzerland varies greatly between different areas. Temperatures are the relatively high on the Swiss Plateau and lower in the Jura Mountains and the Alps (Theurillat and Guisan, 2001).

The potential natural vegetation on the Swiss Plateau, e.g., vegetation that would prevail without human influence in the current climate, would consist of oak-hornbeam (*Quercus-Carpinus*) forest in the lower colline belt and beech (*Fagus*) forest in the higher colline (< 600 m) to submontane belt. Higher up silver fir (*Abies alba*) would be more abundant. In the subalpine belt up to the tree line (between 1800 and 2000 m asl) pine and spruce (*Pinus* and *Picea abies*) would dominate (Burga and Perret, 1998).

In this thesis pollen assemblages from the surface sediment of 31 small lakes are used, as well as assemblages from four large lakes. The sites are indicated in the Figures 1 in Chapter 2, 3 and 5.

Overview of the chapters

In the next section a summary of the results and conclusions of the different chapters is presented. Chapter 2 to 5 have been published in or will be submitted to scientific journals. The chapters are independently written, from each other or from this introduction. Some overlap is, therefore, inevitable.

Pollen Productivity Estimates for quantitative reconstruction of vegetation cover on the Swiss Plateau

A first aim of this study was to determine pollen productivity estimates for herbaceous and tree taxa on the Swiss Plateau, at the same time determining the RSAP for small- to medium-sized lake basins (Chapter 2). Therefore, modern vegetation abundance and pollen deposition were compared for 20 lakes and their catchments. The vegetation abundance around the lakes was surveyed on aerial photographs and in detail in the field. Proportional pollen data from surface sediments were already analysed, reflecting modern pollen deposition.

Thirteen plant taxa were chosen, mostly based on their abundance in the pollen samples (surface sediment). Other taxa were chosen based on their abundances in the present-day vegetation, and their indicator value for different land cover types. Some taxa indicative of

azonal vegetation such as *Salix*, *Alnus*, or *Populus* were excluded. The used taxa were: *Abies alba* (silver fir), *Corylus avellana* (hazel), *Carpinus betulus* (hornbeam), *Compositae* subfamily *Cichorioideae* (composites), *Plantago lanceolata* (narrow-leaved plantain), *Fagus sylvatica* (beech), *Fraxinus excelsior* (ash), *Betula* (birch), *Quercus* (oak), *Picea abies* (spruce) and Poaceae (grasses). *Pinus cembra* and *P. sylvestris*-type were combined as *Pinus* (pine), and Cerealia-type and *Secale cereale* as Cerealia (wheat, oats, barley, rye). Poaceae were used as the reference taxon, i.e., the PPE of Poaceae is set to 1.

For comparison, the PPE were estimated using all three ERV sub-models, as well as three different distance-weighting approaches. The RSAP was found to be the area out to 800 m from the lakeshore, regardless of the applied distance-weighting or ERV sub-model. Most tree species had higher or equal PPE to 1. All herbaceous taxa showed PPE lower than 1, the PPE for Cerealia were even lower than 0.1. The results between the three ERV sub-models differed slightly. The different distance-weighting approaches affected the PPE for *Abies* much more than for other taxa. The taxon-specific Prentice-Sugita model is likely to give the best PPE of *Abies*, because the pollen grain of *Abies* is much heavier than the other taxa.

This study gave evidence that PPE differ between regions. Even when sampling strategies for vegetation and pollen are standardised, pollen productivity can still be influenced by regionally different factors, such as climate, vegetation structure, geology, and soils. In addition, differences at genus or species level may occur between regions.

Evaluating Swiss Pollen Productivity Estimates using a simulation approach

Because the PPE established for the Swiss Plateau differed sometimes from values in other regions in Europe, they were evaluated (Chapter 3). Therefore, pollen assemblages were simulated for eleven Swiss Plateau sites using POLSIM. The sites were independent of the ones used in Chapter 2. The local vegetation composition and abundance was estimated for an area going out to 5 km from the lakeshores. It was derived from a low-resolution land cover map (100 m resolution) that incorporated 12 land cover classes. PPE derived by all three ERV sub-models were used. These were obtained with distance-weighted vegetation using the Prentice-Sugita model and constant wind speed of 3 m s^{-1} . For Cerealia an adjusted PPE-value was used, because the original value was statistically too low to be used. Two approaches were used to incorporate regional vegetation. The first was based on land cover data out to 200 km around the Swiss Plateau. The second was based on averaged values of the afore-mentioned land cover data out to 5 km from the sites. Next, pollen assemblages were simulated by POLSIM. They were compared to observed present-day pollen assemblages at the same sites.

When a regional vegetation estimate based on land cover data out to 200 km was used, the majority of the simulated pollen proportions was within a range of 5% of over- or underestimation compared to the observed values. At eight of the eleven sites the dominant taxon was correctly estimated. The modelled sum of arboreal pollen was correct within $\pm 11\%$ at nine sites. The results using the averaged land cover data going out to 5 km from the sites were less accurate.

The results indicated that the PPE established for the Swiss Plateau (including the adjusted Cerealia-PPE) can be used to simulate pollen assemblages with reasonable accuracy. They may, therefore, be used for other aims, such as reconstructing past vegetation. The use of a more detailed regional vegetation estimate improved the simulations, demonstrating the importance of acquiring an accurate regional vegetation estimate. The results also showed that POLLSCAPE models can be applied in landscapes with relatively complex topographic settings.

Estimating past vegetation openness by pollen-vegetation relationships: a modelling approach

Having the basic tools such as regional PPE and RSAP available, the testing of hypotheses about vegetation openness in the past becomes possible (Chapter 4). For this purpose two simple scenarios of a mid-Holocene landscape in lowland Switzerland were designed. The first consisted of wood pasture driven by the presence of large herbivores. The second consisted of closed woodland containing small gaps where light-requiring trees can regenerate. Next, POLLSCAPE was used to assess these past landscape scenarios using data from the Swiss Plateau. The resulting modelled pollen assemblages were then compared to a typical mid-Holocene pollen record from the Swiss Plateau.

The results suggested that the landscape design based on closed canopy forest had most in common with the mid-Holocene pollen assemblages. However, all simulated pollen assemblages contained higher Poaceae and *Quercus* and lower *Abies*, *Corylus*, and *Betula* pollen proportions than the observed pollen assemblage. The high *Corylus* proportion in the observed pollen assemblage showed that the disturbance area must have been larger than can be expected from the closed forest theory alone. Natural (e.g., river plains, wetlands, poor soils) and disturbance-induced (floods, wind-throw, fire) relatively small openings in closed beech forest may have produced the observed pollen assemblage at Lobsigensee 6000 years ago.

Modelling regional vegetation changes on the Swiss Plateau during the past two millennia

Besides such pure model approaches as used in chapter 4 the available data also allow assessing present-day and past regional vegetation abundance on the Swiss Plateau (Chapter 5) with REVEALS. First, the present-day averaged REVEALS estimate from two large Swiss Plateau lakes was compared to present-day vegetation abundance compiled from land cover data (Land Cover Vegetation estimate, LCV). On the whole, and especially for the Cerealia or the herbaceous species component, the REVEALS estimate matched LCV better than the averaged observed pollen assemblages from the surface sample lake sediments.

A regional vegetation composition for the past two millennia was reconstructed in 200-year intervals using pollen assemblages from three large lakes. The REVEALS results indicated a much higher anthropogenic impact on the vegetation throughout the past 2000 years than the pollen percentage diagrams suggested. The inferred vegetation changes reflected the differences in agricultural and other human activities in the region during the Roman Time, the Migration Period, the early and late Middle Ages, and the onset of Modern Time. With the exception of the Migration Period, cereals covered most of the region of the Swiss Plateau during the past two millennia.

Conclusions

In this thesis Swiss pollen productivity estimates for 13 plant taxa were introduced, evaluated, used for hypothesis testing and the reconstruction of past vegetation. The modern simulation results presented in Chapters 3 and 5, compared well to their observed counterparts and thus provided evidence that the Prentice-Sugita models are able to cope with landscapes characterized by more complex topographical situations. Also, pollen assemblage from small hollows or moss polsters have traditionally been used for determination of PPE (Calcote, 1995; Broström *et al.*, 2004). However, although error margins may be larger, the PPE derived from small to medium-sized lakes are reliable (Chapter 3) and can be used in large lakes to infer past land cover changes (Chapter 5).

In Chapter 5, a regional vegetation reconstruction was made for the past 2000 years. The reconstructions illustrated that the openness of the regional landscape was much higher than expected from the pollen assemblages alone. The results demonstrated the necessity to include the “pollen view of the landscape” when interpreting pollen records.

In Chapter 4, a simulation approach was used to compare conflicting theories about the scale and causes of openness in natural forests. Although the results cannot provide conclusive arguments about the causes of openness, it was demonstrated POLSIM can be used as a tool to test alternative hypotheses. Still, there is much room left for the extending the application of these simulation models. The newly developed tool of LRA opens a wide field of research on the origin and scale of landscape openness in the past and its influence on system earth.

Outlook

The Swiss PPE allow for further testing of openness and vegetation patterns on the Swiss Plateau in the past. When more sites are surveyed, the PPE of more taxa can be calculated and the modelling of past land cover can be extended. The recent development of LOVE enables the estimation of local vegetation assemblages in the order of 1 km around sites on the Swiss Plateau. Such estimates will allow archaeologists to tackle questions about local human impact (fire disturbances, the scale of cultivation and biodiversity change) and ecologists to address nature conservation issues.

The results in this thesis suggest that the landscape of the past two millennia was more open than was initially assumed. Human impact was, therefore, more extended than previously thought. The openness of the landscape had substantial impacts on biophysical factors such as albedo and soil moisture, and needs to be incorporated into climate models. When regional vegetation is estimated at higher temporal resolution and at longer time-scales, more information becomes available about the interaction between land cover and climate change. Furthermore, the comparison between past land cover, erosion rates, and flooding frequencies can provide basic insights for policy makers how the present-day situation differs from the past and how land cover change might help to solve current issues on the Swiss Plateau in a sustainable way.

CHAPTER 2

POLLEN PRODUCTIVITY ESTIMATES FOR QUANTITATIVE RECONSTRUCTION OF VEGETATION COVER ON THE SWISS PLATEAU

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Abstract

Here, we present the first step to reconstruct vegetation cover in Central Europe quantitatively. Modern vegetation and pollen deposition were compared for 20 small to medium-sized lakes and their catchments on the Swiss Plateau, a relatively flat region between the Jura Mountains and the Alps. To correct for the pollen dispersal bias in pollen assemblages, vegetation abundance was distance-weighted using three different approaches. The Relevant Source Area of Pollen (RSAP) and pollen productivity of 13 plant taxa were estimated using three different sub-models of the Extended R-Value model (ERV-model). RSAP was 800 m regardless of the applied distance-weighting or ERV sub-model. Pollen Productivity Estimates (PPE) varied from 10 to lower than 0.1 among pollen taxa and differed slightly between the models. Relative to grasses most trees were higher pollen producers and some were equal producers, whereas the herb taxa showed lower PPE. Generally, PPE from lowland Switzerland differ from those found in other European regions. Sampling strategies of vegetation and pollen samples are a likely cause for this found variation. However, pollen productivity is also influenced by regionally different factors, like climate, vegetation structure, geology, and soil types. In addition, differences at genus or species level may occur between areas. Our comparison between the different regions in Europe shows that PPE of one region may not be directly applicable to other regions.

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Introduction

Over the past millennia a gradual transition from natural environments to cultural landscapes has taken place in Europe (e.g., Messerli *et al.*, 2000). For instance, European forests are now widely accepted as human-shaped ecosystems (Bürigi and Schuler, 2003). It has also been suggested that anthropogenic driven climate change started as early as 8000 years ago with the advent of agriculture and subsequent clearance of forests (Ruddiman, 2003). For these reasons, when assessing driving factors for contemporary and future global change, it is necessary to incorporate and understand the history and dynamics of human impact on the landscape.

In the absence of observational data or historical documents fossil pollen records are commonly used to determine past vegetation composition and land cover. However, quantification of vegetation cover based on pollen analysis is complex. Firstly, differential pollen productivity of plant species and differential dispersal and preservation of pollen grains lead to a bias in representation or even the absence of certain plants in the pollen record (e.g., Prentice, 1988; Jackson, 1994). Secondly, despite constant progress in taxonomical identification of pollen grains (e.g., Punt *et al.*, 2003; Beug, 2004) it is often difficult to identify pollen to species or even genus level. Thirdly, basin size affects the composition of a pollen assemblage: as lake size increases, the influence of local vegetation decreases in favour of pollen originating from regional vegetation (e.g., Andersen, 1970; Janssen, 1973; Jacobson and Bradshaw, 1981).

To assess unbiased estimates of vegetation change using pollen percentages, Davis (1963) introduced the concept of R-values. The R-value was defined as a correction factor for the pollen data to represent vegetation surrounding a sampling site. However, the R-value method did not produce consistent results, because of the small sample size and the lack of a background pollen component. Andersen (1970) proposed a linear model for the relationship between pollen and vegetation abundance, estimating a pollen representation factor, as well as background pollen coming from outside the surveyed vegetation area. Although Andersen's model improved our understanding of the pollen-vegetation relationships greatly, it requires absolute or quasi-absolute pollen data, whereas pollen percentage values are not applicable for the model (Prentice and Parsons, 1983).

In theory, pollen abundance in an absolute unit, such as pollen accumulation rates, would be ideal for quantifying the pollen-vegetation relationship. However, within-lake variation of pollen accumulation rates can be larger than between-lake variation even in the same vegetation region (e.g., Davis and Brubaker, 1973; Ammann, 1989). On the other hand, pollen percentages in lakes and mires are less variable (Davis and Brubaker, 1973), and palynologists still commonly use pollen percentages as a primary tool for interpreting changes in fossil pollen assemblages. Therefore, Parsons and Prentice (1981) and Prentice and Parsons (1983) created the Extended R-value (ERV) models, which expand and generalise Andersen's (1970) model to be able to use pollen percentage data.

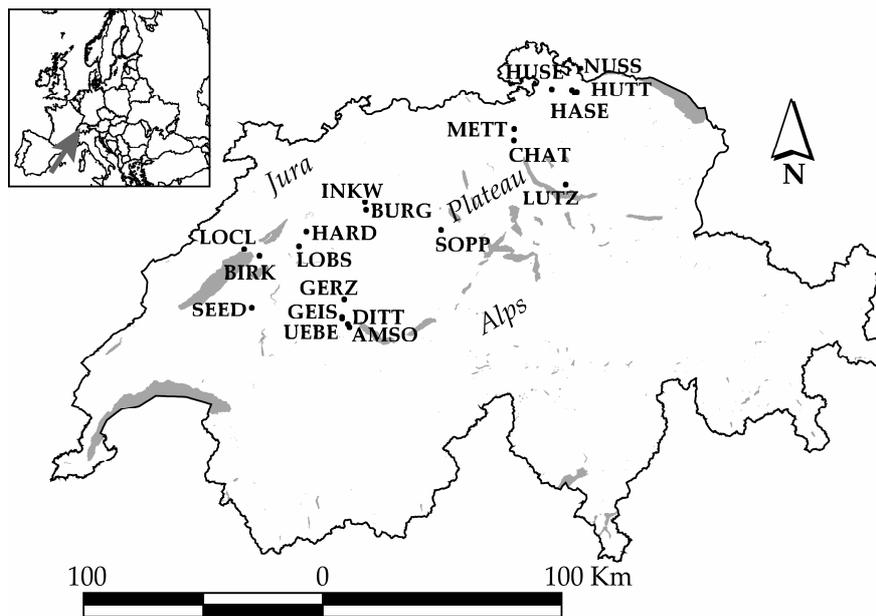


Figure 1 Map of Switzerland with 20 selected lakes at the Swiss Plateau indicated by dots and name codes (see Table 1). In grey large water areas are shown

The outcome of the ERV-models may be further enhanced by incorporating “the pollen sample’s view of the landscape” (Prentice and Webb III, 1986). In a pollen assemblage, the contribution of the vegetation closer to the sampling site is higher than that of vegetation further away; and in similar circumstances, heavier pollen carried by wind will be transported less far from its source plant than lighter pollen. Therefore, vegetation abundance should be distance-weighted before comparing to the pollen data. Prentice (1985) proposed to use a pollen dispersal and deposition model that simulates pollen deposition at a point in the centre of a circular basin. Sugita (1993) adapted the model for pollen deposition over the entire surface of a circular basin.

The Prentice-Sugita model aims to counteract the dispersal and deposition differences between pollen types. If such a distance-weighting model is applied to the vegetation data, the ERV-models give by definition Pollen Productivity Estimates (PPE) instead of a pollen representation factor (Prentice, 1985, 1988; Sugita, 1993). PPE and background pollen, the parameters estimated by the ERV-models, have been inferred for different regions of the world (e.g., Calcote, 1995; Jackson and Kearsley, 1998; Sugita *et al.*, 1999; Broström *et al.*, 2004; Nielsen, 2004; Bunting *et al.*, 2005; Nielsen and Odgaard, 2005).

The purpose of this study was to calibrate pollen-vegetation relationships on the Swiss Plateau, thus estimating PPE, background pollen, and the distance that divides local from regional source vegetation, as a first step for quantitatively assessing human impact on past land cover changes in Central Europe. Despite previous attempts to relate pollen to tree cover (e.g., Dambach, 1998; van der Knaap and van Leeuwen, 1998), quantitative pollen-vegetation relationships have not been determined for this region.

Modelling pollen-vegetation relationships

Extended R-value models (ERV-models)

The basic assumption underlying the ERV-models is that there is a linear relation between the absolute pollen deposition in a sedimentary basin and the vegetation abundance in an absolute unit surrounding the basin (Parsons and Prentice, 1981; Prentice and Parsons, 1983). Pollen productivity and background pollen are, in theory, the slope and the intercept of this linear relationship when vegetation is distance-weighted (Prentice, 1985; Sugita, 1993, 1994). However, non-linearity occurs (the Fagerlind effect) when either pollen data or vegetation abundance data are expressed as percentages (Fagerlind, 1952; Davis, 1963; Parsons and Prentice, 1981; Prentice and Parsons, 1983; Prentice and Webb III, 1986; Jackson, 1994); an increase in pollen percentages of a given taxon does not necessarily imply an increase in vegetation percentage of the same taxon, and vice versa. Also, even if pollen productivity is assumed constant for a plant taxon, the slope of the pollen-vegetation relationship can differ in different vegetation types when pollen percentages are used (Davis, 1963). However, the ERV-models are constructed in such a way that the linear pollen-vegetation relationship can be obtained from pollen percentage data by correcting for the Fagerlind effect (Parsons and Prentice, 1981; Prentice and Parsons, 1983; Sugita, 1994; Jackson *et al.*, 1995).

The goodness of fit between deposited pollen and vegetation abundance will improve with increasing area of surveyed vegetation around a sampling site. At a certain distance, however, the correlation between pollen and vegetation will not improve further. This distance is by definition the relevant source distance of pollen (Sugita, 1994). Likewise, the area from the edge of the sampling basin (i.e., lake, mire, or moss polster) to the relevant source distance is called the Relevant Source Area of Pollen (RSAP).

Currently, there are three different sub-models of the ERV-model available. These sub-models have different site factors to adjust for the use of the proportional pollen or vegetation data. Sub-model 1 and 2 use pollen and vegetation percentages (Parsons and Prentice, 1981; Prentice and Parsons, 1983), whereas pollen percentages and plant abundance data expressed in absolute units (e.g., such as cover or biomass per area) are used in sub-model 3 (Sugita, 1994).

Pollen dispersal and deposition

Several methods have been proposed to weigh the plant abundance in relation to the distance from the lakeshore, for instance, by step-wise inverse weighting ($1/d$, where d = the distance from the lakeshore) or stepwise inverse squared-distance (Calcote, 1995; Jackson and Kearsley, 1998). A stepwise taxon-specific model based on an atmospheric diffusion model was proposed by Prentice (1985) and Sugita (1993), Sugita *et al.* (1997; 1999), extensively reviewed in Jackson (1994) and Jackson and Lyford (1999). The Prentice-Sugita model takes basin size, wind speed and variation in fall speed of pollen grains into account. The basic assumptions (Prentice, 1985; Sugita, 1993, 1994; Sugita *et al.*, 1997) are that lakes are circular, that there is no height-difference in the landscape nor between plants, and that wind is equal from all directions. The vegetation at certain stepwise increasing distances from the lakeshore is averaged for that distance, regardless of the direction from the site. Pollen dispersal

and deposition at a basin is estimated considering that pollen deposition is decreasing arc-wise with increasing distance from the source plant, the function derived from an atmospheric diffusion model of small particles from a source at ground level (Sutton, 1953).

Prentice's (1985) model is used for pollen deposition at the centre of a sedimentary basin, thus appropriate for pollen deposition on mires and fens where pollen grains will not move once deposited. Sugita (1993) and Sugita *et al.* (1997; 1999) modified Prentice's model to approximate for the pollen deposition on the entire surface of a sedimentary basin. Sugita's model is appropriate for pollen deposition on lakes and ponds, because of mixing of pollen in their water body (Davis, 1973).

Material and methods

Study area

The Swiss Plateau is situated between the Jura Mountains in the northwest of Switzerland and the Alps in the south (Figure 1). The Plateau was mainly shaped by advancing and retreating Alpine glaciers during the Pleistocene. Its surface is mostly undulating to rolling, sometimes hilly. Elevation ranges between 300 and 800 m asl.

The Swiss Plateau is the most productive agricultural area in Switzerland. Although the total agricultural area is declining, it still occupies nearly half of the Swiss Plateau (SFSO, 2001). Wooded areas represent almost a quarter of the landscape. They consist mainly of European

Table 1 Characteristics of the sampled lake basins

Site	Code	Elevation (m asl)	Water depth (m)	Latitude (dec. degrees)	Longitude (dec. degrees)	Surface area (ha)	Av. radius (m)
Amsoldingensee	AMSO	640	12.5	46.72342	7.57598	38.26	349
Birkenhof Weiher	BIRK	430	2.7	46.99136	7.08053	2.30	85
Burgäschisee	BURG	470	31.0	47.16831	7.66813	20.85	258
Unterer Chatzensee	CHAT	440	7.8	47.43158	8.48943	18.71	244
Dittligsee	DITT	660	16.5	46.75584	7.53484	5.92	137
Geistsee	GEIS	670	6.4	46.76142	7.53511	0.93	54
Gerzensee	GERZ	600	10.0	46.83072	7.54709	25.26	284
Weiher bei Hardern	HARD	500	4.5	47.08675	7.33808	0.73	48
Hasensee	HASE	430	5.5	47.60696	8.83172	10.46	182
Husemer See	HUSE	420	14.0	47.62169	8.70439	7.70	157
Hüttwiler See	HUTT	430	15.0	47.60974	8.84377	34.40	331
Inkwilersee	INKW	470	5.0	47.19823	7.66298	10.16	180
Lobsigensee	LOBS	520	2.5	47.03087	7.29839	2.26	85
Le Loclat	LOCL	440	9.2	47.01904	6.99703	4.51	120
Lützelsee	LUTZ	500	6.0	47.25932	8.77178	12.06	196
Mettmenhasler See	METT	420	12.5	47.47405	8.49192	2.49	89
Nussbaumer See	NUSS	440	8.2	47.61691	8.81622	25.09	283
Lac de Seedorf	SEED	610	7.5	46.79522	7.04045	9.72	176
Soppensee	SOPP	600	27.0	47.09096	8.08135	23.32	272
Übeschisee	UEBE	650	14.5	46.73423	7.56587	14.04	211

beech (*Fagus sylvatica*), Silver fir (*Abies alba*), and plantations of Norway spruce (*Picea abies*). Settlements and urban areas presently utilise about 15% of the total area, while 10% is covered with lakes and rivers or otherwise unproductive areas (SFSO, 2001).

In the past millennia, the area has known major deforestation and afforestations phases, attributed for instance to Roman settlements, the Migration Period and the Middle Ages (e.g., Rösch *et al.*, 1992). Bürgi (1999) assumes that the pattern of forests and open landscapes in the Swiss lowlands probably is the same as in the Middle Ages, although the land use and vegetation composition has changed.

Site selection

The Swiss Plateau is possibly the best area in Switzerland to establish pollen-vegetation relationships using the ERV-models and the Prentice-Sugita model. The area is relatively flat and there is a high pollen data availability, concerning surface sediment samples as well as longer pollen records. Twenty lakes in Switzerland were selected (see Figure 1) with an average lake radius less than 300 m, and no steep slopes occurring within the first kilometre around the lake. Table 1 shows the characteristics of the selected sites.

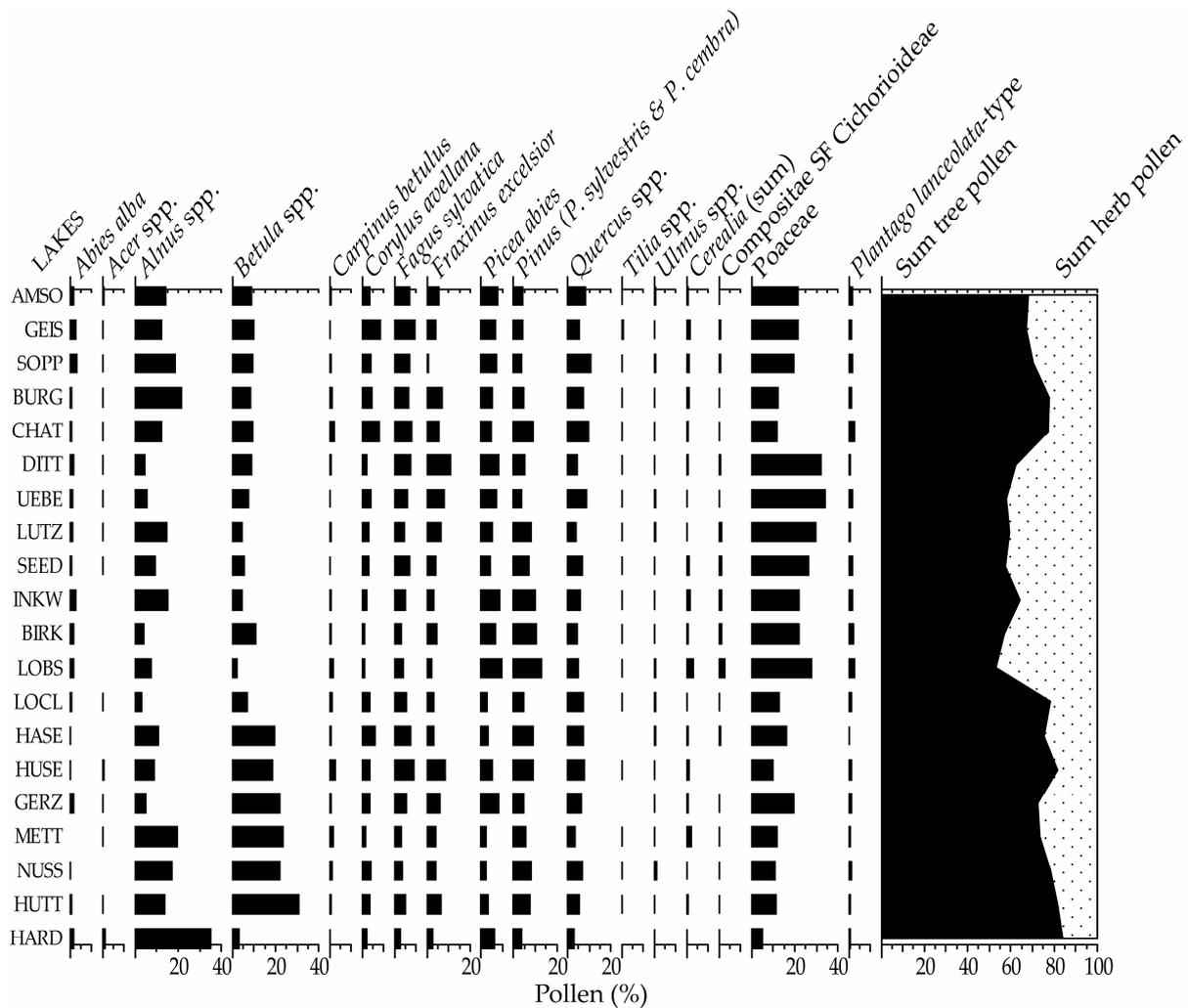


Figure 2 Surface sample pollen diagram of 20 selected lakes at the Swiss Plateau

Pollen data

The pollen data used here were selected from four previously performed studies. All lakes were sampled either in 1993/1994 (Lotter *et al.*, 1997a; van der Knaap and van Leeuwen, 1998) or in 1999 (Guthruf *et al.*, 1999). Surface sediments were collected with a gravity corer from either the centre or deepest part of the lake, the top 1 cm was extruded in the field and used for further analysis. The surface sediment sample of Lobsigensee was disturbed and instead a sample was used taken at 5 cm in core LQ-120 by Amman (1989). All sediment samples were treated with conventional palynological methods (e.g., van der Knaap *et al.*, 2000) and J. van Leeuwen counted all the samples, except for Lobsigensee. The minimum pollen sum was 700 pollen grains (excluding aquatics), comprising 185 identified pollen and spore types. The pollen percentages of major taxa are shown in Figure 2. The sites differ to each other with respect to local land cover.

In the ERV-programs, we simultaneously estimate pollen productivity and background pollen for each taxon. Statistically speaking, the number of sites, therefore, ought to be at least twice the number of taxa used. Using less than the optimal number of sites affects the standard deviations of the PPE mostly, since they become larger. We selected thirteen taxa (see Table 2), mostly based on their abundance in modern and fossil pollen samples, but also based on their abundances in the present-day vegetation, and their indicator value for different land cover types. Some taxa indicative of azonal vegetation such as *Salix*, *Alnus* or *Populus* were excluded. For the data analysis, we combined *Pinus cembra* and *P. sylvestris*-type as *Pinus*, and Cerealia-type and *Secale cereale* as Cerealia.

Fall speed of pollen

The dispersal distance of pollen is influenced by its fall speed. Empirical estimates of the fall speed of pollen are available for some tree species (e.g., Dyakowska, 1936; Eisenhut, 1961; Gregory, 1973). However, for herbaceous taxa we have to use pollen fall speed estimates based on Stokes' law for pollen that are assumed to be smooth spheres (Gregory, 1973; Sugita *et al.*, 1999; Broström *et al.*, 2004). The chosen empirical and the calculated estimates are displayed in Table 2. Note that for *Pinus* an average value of *P. cembra* and *P. sylvestris*-type (Dyakowska, 1936) was taken.

The fall speed of pollen for Cerealia was estimated as follows: first we calculated the fall speed for *Secale cereale*, *Triticum aestivum*, *Hordeum vulgare*, and *Avena sativa* individually, using mean diameters of 48.45, 54.40, 44.45 and 52.10 μm (Beug, 2004). For all species a shape factor of 1 (Sugita *et al.*, 1999) and pollen density of 1.1 g cm^{-3} similar to *Zea mais* (Gregory, 1973) was assumed. Then, the averaged value of 0.0782 m s^{-1} was used as the fall speed for Cerealia pollen types.

Table 2 Pollen fall speed per taxon

Pollen taxa	Fall speed (m s^{-1})
<i>Abies alba</i>	0.120 ^a
<i>Betula (pendula)</i>	0.026 ^a
<i>Carpinus betulus</i>	0.042 ^a
<i>Corylus avellana</i>	0.025 ^b
<i>Fagus sylvatica</i>	0.055 ^b
<i>Fraxinus excelsior</i>	0.022 ^a
<i>Picea abies</i>	0.056 ^a
<i>Pinus (sylvestris and cembra)</i>	0.041 ^c
<i>Quercus (robur)</i>	0.035 ^a
Cerealia	0.078 ^d
Comp. SF. Cichorioideae	0.051 ^e
<i>Plantago lanceolata</i> -type	0.029 ^e
Poaceae	0.035 ^f

^aEisenhut (1961); ^bKnoll (as cited in Gregory, 1973); ^cDyakowska (1936); ^dthis study; ^eBroström (2002); ^fSugita *et al.* (1999).

Vegetation survey

Detailed digital colour aerial photographs were analysed for land cover in a one-kilometre radius around each of the 20 selected lakes, first by a classification tool in remote sensing software, then corrected visually. The aerial photographs had a resolution of circa 0.5 m. They were taken in the summer of either 1998 or 2002. Before classification the aerial photographs were geo-referenced and ortho-rectified to the level of digitised 1:25 000 topographic maps. The root mean square error of the geo-reference models was minimised to 10 m.

Eight land cover and land use classes were distinguished in the photographs: hay meadow, pasture, cereal cultivation, other agriculture, wetlands, non-pollen producing areas (e.g., settlements), open water surfaces, and forest. The spatial distribution of forest and open land (hay meadow, pasture, cereal cultivation and other agriculture) was confirmed by topographic maps and ground truthing. However, the seasonal and/or annual rotation schemes of the agricultural fields prevented exact ground truthing of the agricultural land use types.

We surveyed vegetation composition within the classified land cover and land use classes in July 2003. The plant identification in the field was adapted to the taxonomic level of pollen identification. We estimated percentage cover for each taxon within an entire field, forest, or thicket. Total cover values in individual cover types may exceed 100% because of multiple vegetation layers. Although there is subjectivity involved in visual cover estimation, we minimized the surveyors' bias between sites by using only one group of surveyors. Most forests, thickets, and some hedges in a one-kilometre radius of each lake were surveyed, resulting in 215 records. Furthermore, 54 hay meadows and pastures were surveyed.

Based on a TWINSPLAN analysis (Hill *et al.*, 1975; Hill, 1979) of the vegetation data, the surveyed forests, thickets, and hedgerow trees were divided into five classes (silver fir forest, ash-oak forest, beech-spruce forest, wet forest, and trees). These could also be located on the land use map. Vegetation composition of the 12 land cover and land use classes was based on averaged values of the specific vegetation compositions surveyed.

Spatial analysis of the land cover data was done within the GIS-program ArcView. The mean area percentage of each land cover class was calculated between concentric rings around the lake borders that were 10 m apart. Using vegetation composition per land cover class, mean plant area percentages per stepwise increasing distance from the lakeshore were calculated in a spreadsheet.

Program and settings

We used a slightly modified version of the ERV-program introduced by Sugita *et al.* (1999), called ERV.v.6.0HAM200. The program needs input data concerning vegetation abundance and pollen characteristics, but also other factors are taken into account, such as wind speed, lake radii, and an estimate of the maximum distance where pollen come from. Furthermore, the ERV sub-model and vegetation distance-weighting method are specified.

For pollen productivity estimation, ideally circular lakes of equal size should be used, because in theory these have RSAP that are also equal in size. The lakes in our dataset are,

however, not always circular-shaped. Their radius was calculated based on their surface area. Lake radii varied from 50 to 300 m. Then an average radius was taken for all lakes (190 m) and the distance classes of the vegetation data were accordingly adjusted. Because of the stretching or shrinking of the surface area in the vegetation data, the area represented by certain plants may thus be over- or underestimated.

Approximation of wind speed is difficult, since pollen dispersal and deposition might be most influenced by maximum wind speeds at the time of flowering. Not only wind speed, but also wind direction influences pollen dispersal and deposition. However, the Prentice-Sugita model assumes that wind speed remains constant and is equally in size from all direction. We therefore used the Prentice-Sugita model with wind speeds of 3 and 4 m s⁻¹ and compared the results. Two non-species specific methods for distance-weighting were also applied, namely vegetation abundance divided by distance or by squared distance (e.g., Calcote, 1995).

The regional source area was assumed 400 km from the centre of the region. The same setting of parameters was used to calculate vegetation abundance for all three ERV sub-models. Next, pollen productivities of individual taxa relative to Poaceae (i.e., pollen productivity of Poaceae is set to 1) were estimated for every stepwise distance. PPE were determined at the RSAP, at the distance where the likelihood function score of the maximum likelihood method approaches an asymptote (Sugita, 1994).

Results and discussion

Relevant Source Area of Pollen

In Figure 3 the likelihood function scores are plotted against distance from the lakeshore for the three ERV sub-models and vegetation distance-weighted with the Prentice-Sugita model and wind speed 3 m s⁻¹. This graph is representative for the graphs derived from the other distance-weighting methods, which are therefore not shown. Regardless of the ERV-program settings, the asymptote is reached around 800 m distance from the lakeshores. We therefore conclude that the RSAP of the studied small lakes with an average lake radius of 190 m is 800 m from the lakeshore.

Theoretical and empirical studies have shown that RSAP is strongly influenced by basin size and vegetation heterogeneity. For instance, the RSAP of moss polsters and forest hollows is between 50 and 400 m (e.g., Sugita, 1994; Calcote, 1995; Broström *et al.*, 2005; Bunting *et al.*, 2005), whereas for lakes RSAP between 600 to 1700 m have been found (e.g., Sugita, 1994; Sugita *et al.*, 1999; Nielsen and Sugita, 2005).

However, RSAP is also influenced by patterning of the vegetation within a landscape (Sugita, 1994; Calcote, 1995; Sugita *et al.*, 1999; Bunting and Middleton, 2005). Calcote (1995) found for northern USA that variation in vegetation patch size affected the RSAP: larger patches caused a larger RSAP. Simulations by Sugita *et al.* (1999) indicated a larger RSAP (1000 m) in the semi-open landscape of southern Sweden compared to the open landscape (800 m), because of larger vegetation patches. These findings were confirmed by Bunting *et*

al. (2004) in a study that evaluated the effect of pollen taxa characteristics and patterning in the landscape on the RSAP. They also showed that for basins of a given size and under fixed atmospheric conditions, vegetation patch size and cell size in the simulation landscapes were the two most important parameters influencing RSAP.

The observed RSAP for small lakes on the Swiss Plateau is in the same range as simulated for northern USA (Sugita, 1994) and southern Sweden (Sugita *et al.*, 1999). There, RSAP between 600 - 1000 m were simulated for lakes with a 100 to 250 m radius. However, historical landscape modelling of the RSAP in Denmark (Nielsen, 2004; Nielsen and Sugita, 2005) suggested a past RSAP of 1700 m.

It is possible that the differences observed between the Danish and the Swiss dataset, although both empirically derived for lakes, are due to differences in the landscapes and the way they are represented (e.g., cell size, number of vegetation classes, etc.). The vegetation patch size on the Swiss Plateau may be smaller than in Denmark, since its landscape shows more relief. Also, the Swiss land cover maps are based on modern day aerial photographs and are likely to contain more detail than the historical land cover maps from AD 1800 in Denmark. Therefore, it is likely that the so derived RSAP is smaller.

Nielsen and Sugita (2005) also observed that the selection of taxa included in the analysis affects the RSAP. When several plant taxa are grouped, the classification of vegetation patches is affected and patch sizes may become larger, increasing the RSAP accordingly.

Pollen-vegetation relationships

The ERV-models try to find the best linear relationship between pollen and vegetation by adjusting the parameters, i.e., PPE and background pollen. The resulting relationships are shown in Figure 4, as well as the original data, adjusted according the ERV sub-model. Here, only the results are depicted derived with distance-weighted vegetation according the Prentice-Sugita model (wind speed of 3 m s^{-1}) out to 800 m from the lakeshores.

There is considerable variability between the taxa with regard to the ranges of vegetation and pollen percentages. Poaceae have the largest range in both vegetation and pollen, justify-

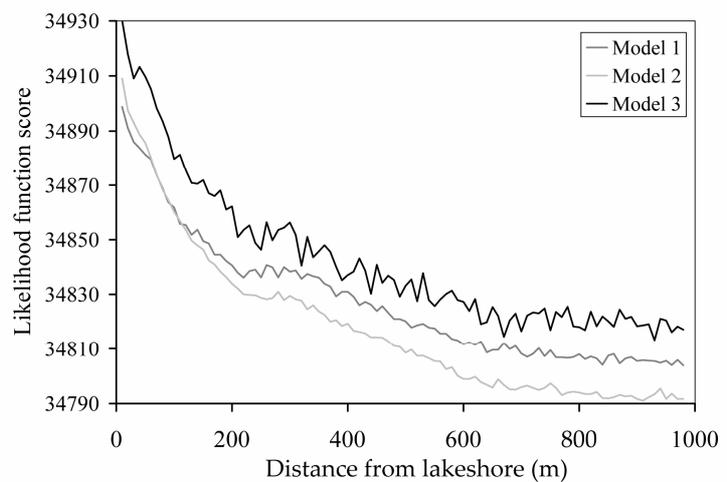


Figure 3 Likelihood function scores for sub-models 1, 2 and 3, by distance-weighting vegetation with the Prentice-Sugita model and wind speed 3 m s^{-1} . The RSAP can be estimated as the area within the distance where the likelihood function score approaches an asymptote and does not further improve (Sugita, 1994)

ing their use as reference taxon. *Abies* and *Carpinus* on the other hand have a very narrow vegetation range. *Cerealia* is standing out because of its broad vegetation range, but narrow pollen range.

The background component varies among taxa and sites. The maximum likelihood estimates of background pollen loading (sub-model 3) can be translated into pollen proportions by dividing the pollen loading of each taxon by the total relative pollen loading at each site (Calcote, 1995). The background percentages vary from site to site, but the averaged background pollen percentages approximate the average amount of pollen of each taxon coming from beyond the RSAP. On average, *Betula*, *Fagus*, and *Pinus* form the bulk of the background component, with each about 8%. Next are *Quercus* and *Picea* with over 5%. The sum of all proportions can be used as an estimate of the percentage of total pollen coming from beyond the RSAP (Calcote, 1995) and amounts up to 46%.

Table 3 presents PPE of all distance-weighting settings and all ERV-models. The PPE are given as an averaged value of the estimates beyond 800 m from the shores of the lakes, to compensate for small variation in the PPE after 800 m. We will first discuss the pollen productivities that were estimated using the Prentice-Sugita model with an applied wind speed of 3 m s^{-1} .

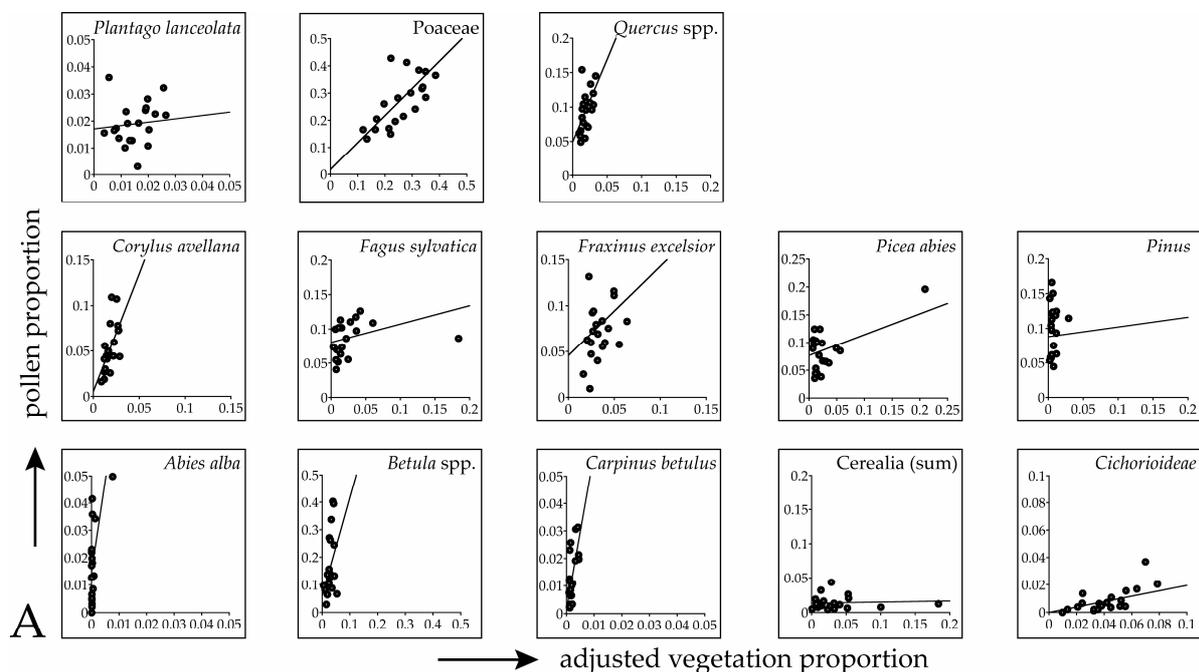


Figure 4 Scatter plots of pollen and vegetation data within an 800m radius (13 taxa included in the analysis). The dataset includes 20 sites. The linear pollen-vegetation relationship found at this distance is depicted with a line. A) Sub-model 1, pollen proportions and adjusted vegetation proportions, B) Sub-model 2, adjusted pollen proportions and vegetation proportions, C) Sub-model 3, relative pollen loading and absolute vegetation abundances

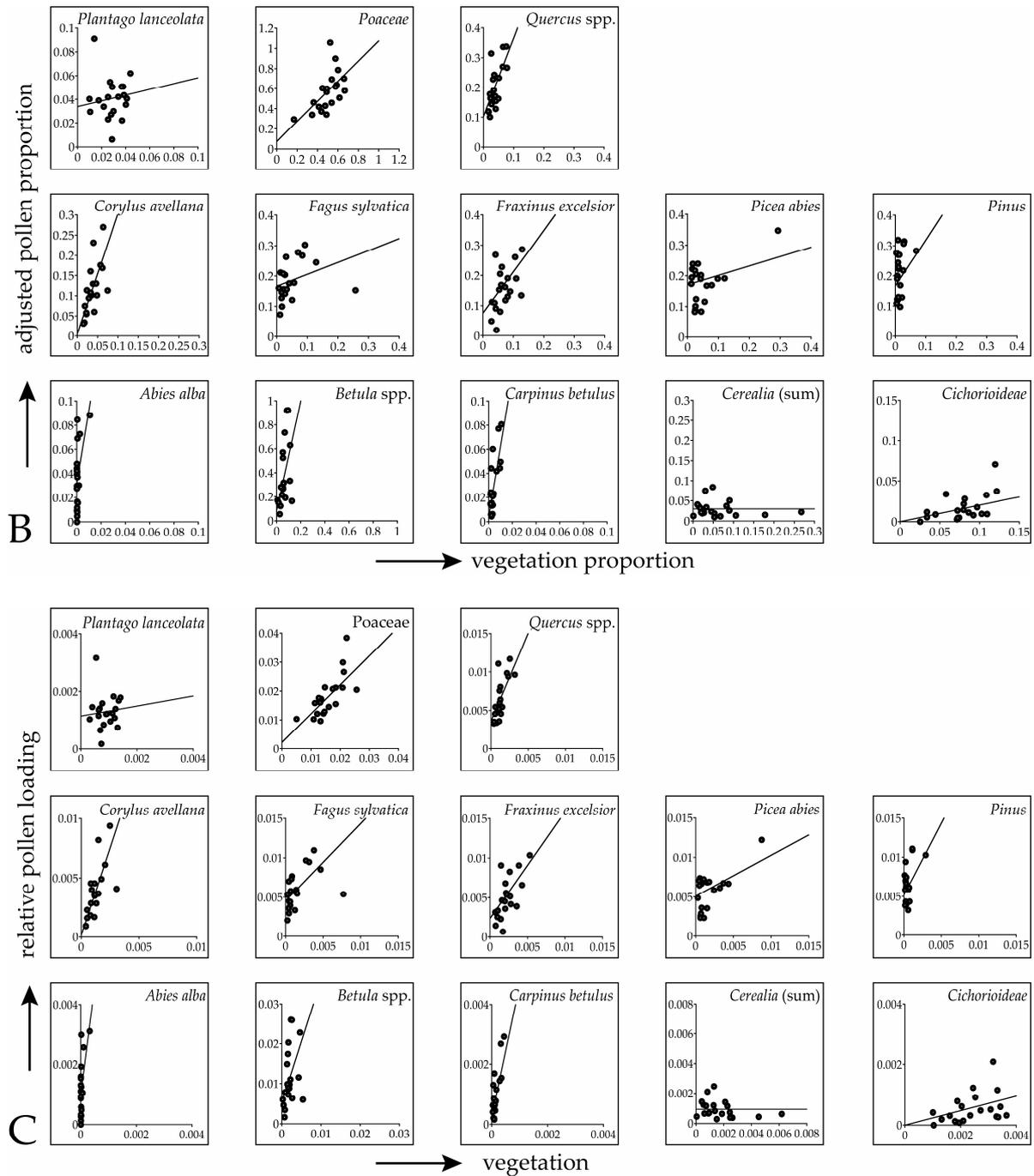


Figure 4 continued

There are three groups recognisable, namely a group of high pollen producers, a group similar to *Poaceae*, and a group of low pollen producers. *Abies* is the highest pollen producer and its PPE vary between 6.53 (sub-model 2) and 9.92 (sub-model 3). It may seem surprising that *Abies* is such a high pollen producer, considering its low presence in the pollen assemblages. However, the fall speed of an *Abies* pollen is very fast (0.12 m s^{-1}), justifying the high PPE.

Carpinus has the second highest PPE, between 4.56 (sub-model 3) and 5.40 (other models). *Betula* is the third highest pollen producer for sub-models 1 and 2 (4.39 and 4.73). However,

its PPE is much lower for sub-model 3 (2.42). For *Corylus* and *Quercus* the model results are quite similar, *Corylus* (2.58 - 3.10) producing a little more than *Quercus* (2.56 - 2.76).

Fagus, *Fraxinus*, *Picea*, and *Pinus* are tree taxa that produce equally to or less than *Poaceae*. The PPE for *Pinus* are varying between models: sub-model 1 gives a PPE of 0.72, sub-model 2 gives 1.76, and sub-model 3 gives 1.35. For *Fraxinus* sub-model 1 is also below 1 (0.77), but sub-models 2 and 3 are above 1 (1.30 and 1.39 respectively). *Fagus* is a low pollen producer with values between 0.41 (sub-model 1) and 0.76 (sub-model 3). PPE of *Picea* are small, between 0.35 (sub-model 1) and 0.57 (sub-model 3). The sometimes high pollen abundance of *Picea* and *Pinus* in Swiss pollen assemblages cannot be explained by their small PPE. However, a large portion of *Picea* and especially *Pinus* pollen is assigned to the background component. This is in agreement with the distribution of these trees in Switzerland, where *Picea* and *Pinus* are most frequently found at higher altitudes (i.e., in the area surrounding the Swiss Plateau).

The herbaceous taxa used in this study were all lower pollen producers than *Poaceae*. The PPE of *Plantago lanceolata* are between 0.09 and 0.24, and those of the Composites are between 0.17 and 0.20. Cerealia has the lowest PPE, ranging from 0.00007 (sub-model 3) to 0.018 (sub-model 1). Particularly, pollen counts of Cerealia are very low relative to its abundance in the vegetation, resulting in the very low estimates of pollen productivity. Such low PPE will hamper the quantification of past vegetation, since a small increase in the number of Cerealia pollen will then have dramatic effects on the vegetation reconstruction, and errors in the prediction will become larger.

Broström *et al.* (2004) found consistently higher values for sub-model 3 compared to sub-models 1 and 2. However, we do not observe such a tendency in our results. Overall, the differences between the sub-models are still within the range of their standard deviations. An exception is the *Betula* estimate of sub-model 3. This is a much lower value than sub-model 1 and sub-model 2. On the other hand, the background component of *Betula* for sub-model 3 is the highest among the included taxa, whereas that is not the case for the other two sub-models.

Sub-models 1 and 2 produce comparable PPE results and differ only for *Pinus*. Besides the low estimate for *Betula*, sub-model 3 produces an intermediate estimate for *Pinus* and the highest estimates for *Abies*. Increasing the wind speed in the Prentice-Sugita model does also not result in certain models having consistently higher or lower values. However, not using the Prentice-Sugita model makes the differences between the estimates of the sub-models larger, hence decreasing the robustness of the model outcomes.

The effect of distance-weighting methods on pollen-vegetation relationships has been studied by several authors (e.g., Prentice, 1985; Jackson and Lyford, 1999; Sugita *et al.*, 1999). Here, three methods of distance-weighting have been used: the Prentice-Sugita model (wind speed of 3 or 4 m s⁻¹), the inverse distance and inverse squared-distance.

Table 3 Pollen Productivity Estimates for four different types of distance-weighted vegetation abundances* and three different ERV sub-models, using Poaceae as reference taxon (set to 1)

Taxon	DW*	ERV sub-model 1		ERV sub-model 2		ERV sub-model 3	
<i>Abies alba</i>	PS 3	7.05	± 1.38	6.53	± 1.34	9.92	± 2.86
	PS 4	3.30	± 0.84	3.28	± 0.87	4.10	± 0.96
	d ⁻¹	0.76	± 0.12	0.68	± 0.14	0.68	± 0.11
	d ⁻²	0.77	± 0.21	0.68	± 0.14	0.72	± 0.15
<i>Betula</i>	PS 3	4.39	± 0.50	4.73	± 0.39	2.42	± 0.39
	PS 4	5.41	± 0.59	5.32	± 0.32	2.92	± 0.35
	d ⁻¹	7.65	± 1.11	5.81	± 0.39	3.24	± 0.33
	d ⁻²	6.35	± 0.79	4.92	± 0.30	1.85	± 0.43
<i>Carpinus betulus</i>	PS 3	5.40	± 0.84	5.40	± 0.61	4.56	± 0.85
	PS 4	5.20	± 0.92	5.04	± 0.56	4.06	± 0.79
	d ⁻¹	5.13	± 0.95	4.87	± 0.71	3.93	± 0.58
	d ⁻²	5.98	± 1.16	5.79	± 0.58	4.18	± 0.99
Cerealia	PS 3	0.02	± 0.01	0.001	± 0.003	0.0007	± 0.002
	PS 4	0.02	± 0.02	0.003	± 0.008	0.0008	± 0.003
	d ⁻¹	0.005	± 0.004	0.0004	± 0.0009	0.0006	± 0.001
	d ⁻²	0.003	± 0.002	0.0001	± 0.0001	0.003	± 0.007
Comp. SF	PS 3	0.20	± 0.01	0.20	± 0.02	0.17	± 0.03
Cichorioideae	PS 4	0.17	± 0.01	0.17	± 0.02	0.13	± 0.04
	d ⁻¹	0.15	± 0.01	0.12	± 0.02	0.08	± 0.02
	d ⁻²	0.16	± 0.01	0.14	± 0.02	0.09	± 0.03
	PS 3	3.10	± 0.25	3.05	± 0.30	2.58	± 0.39
<i>Corylus avellana</i>	PS 4	3.66	± 0.37	3.49	± 0.33	2.97	± 0.41
	d ⁻¹	4.58	± 0.57	3.83	± 0.39	3.54	± 0.45
	d ⁻²	4.86	± 0.57	3.73	± 0.33	2.26	± 0.33
	PS 3	0.41	± 0.12	0.54	± 0.09	0.76	± 0.17
<i>Fagus sylvatica</i>	PS 4	0.36	± 0.10	0.52	± 0.10	0.53	± 0.14
	d ⁻¹	0.32	± 0.08	0.54	± 0.09	0.54	± 0.06
	d ⁻²	0.35	± 0.09	0.57	± 0.09	0.38	± 0.06
	PS 3	0.77	± 0.17	1.30	± 0.22	1.39	± 0.21
<i>Fraxinus excelsior</i>	PS 4	1.04	± 0.35	1.64	± 0.20	1.65	± 0.15
	d ⁻¹	1.36	± 0.28	2.06	± 0.19	2.07	± 0.24
	d ⁻²	1.65	± 0.39	2.30	± 0.24	1.53	± 0.29
	PS 3	0.45	± 0.11	0.35	± 0.08	0.57	± 0.16
<i>Picea abies</i>	PS 4	0.37	± 0.07	0.29	± 0.06	0.40	± 0.07
	d ⁻¹	0.32	± 0.06	0.25	± 0.06	0.33	± 0.05
	d ⁻²	0.33	± 0.07	0.29	± 0.05	0.34	± 0.09
	PS 3	0.72	± 0.31	1.76	± 0.34	1.35	± 0.45
<i>Pinus</i>	PS 4	0.81	± 0.32	1.91	± 0.32	1.29	± 0.45
	d ⁻¹	1.66	± 0.73	2.92	± 0.44	2.37	± 0.32
	d ⁻²	0.95	± 0.59	1.99	± 0.26	0.88	± 0.39
	PS 3	0.21	± 0.11	0.09	± 0.07	0.24	± 0.15
<i>Plantago lanceolata</i>	PS 4	0.26	± 0.12	0.08	± 0.12	0.17	± 0.17
	d ⁻¹	0.21	± 0.08	0.08	± 0.07	0.14	± 0.13
	d ⁻²	0.24	± 0.14	0.10	± 0.10	0.24	± 0.15
	PS 3	2.60	± 0.40	2.76	± 0.33	2.56	± 0.39
<i>Quercus</i>	PS 4	2.75	± 0.54	2.88	± 0.28	2.64	± 0.46
	d ⁻¹	2.92	± 0.47	3.11	± 0.45	3.07	± 0.37
	d ⁻²	3.49	± 0.83	3.40	± 0.38	2.07	± 0.43

*The method used to distance weight the plant abundance. PS means Prentice-Sugita model, with the used wind speed in m s⁻¹; d denotes distance, e.g. (distance)⁻¹ or (distance)⁻².

Although the Prentice-Sugita model is theoretically still the best method to distance-weight vegetation, it was criticized by Jackson and Lyford (1999). Their main critique was that pollen dispersal takes place in unstable atmospheric conditions, whereas Sutton's equation as used in the Prentice-Sugita model, is based on stable conditions. They simulated that in unstable conditions pollen dispersal was more widespread than in neutral conditions. We tried to incorporate these effects by setting a higher wind speed, because we assume that this will have a similar effect on pollen dispersal and deposition as effects of an unstable atmosphere.

Nielsen (2004) observed in her simulations that increasing wind speed increased pollen deposition of taxa with high pollen fall speed, such as *Pinus*, *Picea*, and *Cerealia*. Increased pollen deposition will cause the PPE to decrease. We observed for all ERV sub-models that the effect of setting a higher wind speed was most noteworthy for the very heavy pollen taxon *Abies*. However, PPE for the other taxa, including *Pinus*, *Picea*, and *Cerealia* did not change significantly.

Stepwise inverse distance and stepwise inverse squared-distance are rough approximations for taxon-specific distance-weighting methods. Calcote (1995) suggested that weighting by the inverse squared-distance was a good alternative for the Prentice-Sugita model. However, our results show that the dispersal characteristics of a heavy pollen type have large effects on the pollen productivity estimate of that taxon. It might, therefore, be preferable to use taxon-specific distance-weighting that considers these dispersal characteristics.

Comparison of Pollen Productivity Estimates in Europe

PPE obtained with a similar methodology to our study are available from the USA, UK, and Scandinavia (e.g., Calcote, 1995; Hjelle, 1998; Jackson and Kearsley, 1998; Sugita *et al.*, 1999; Broström *et al.*, 2004; Nielsen, 2004; Bunting *et al.*, 2005). Calcote (1995) already suggested that pollen productivity of species might not be constant between regions, because of unique combinations of climate variables, species competition, or different age, size and genotypes. Pollen productivity may also differ between regions due to other regionally different factors like geology, soil types, or vegetation cover density. Also, for some pollen types, including Poaceae, a number of different species are involved.

We attempt to compare different PPE from various regions. However, it is difficult to find an 'unbiased' reference taxon where PPE are available for in all the regions. Preferably, a taxon that is distinguishable at species level, like *Fraxinus excelsior* or *Picea abies* should be used. We will compare the interregional PPE re-referenced to *F. excelsior* where possible.

Figure 5 shows a comparison of PPE found in this study, as well as previous results from Sweden (Sugita *et al.*, 1999; Broström *et al.*, 2004), Denmark (Nielsen, 2004), and the UK (Bunting *et al.*, 2005). Moss polsters were used to estimate pollen productivity in southern Sweden (Sugita *et al.*, 1999; Broström *et al.*, 2004). The Swedish values for *Pinus* and *Picea* are derived from Prentice *et al.* (1987) and recalculated into PPE (Sugita *et al.*, 1999). For Denmark PPE were determined for groups of taxa using historical maps and subfossil pollen assemblages from small lakes (Nielsen, 2004). British PPE are available from Bunting *et al.* (2005), for two different areas in Norfolk (moss polsters).

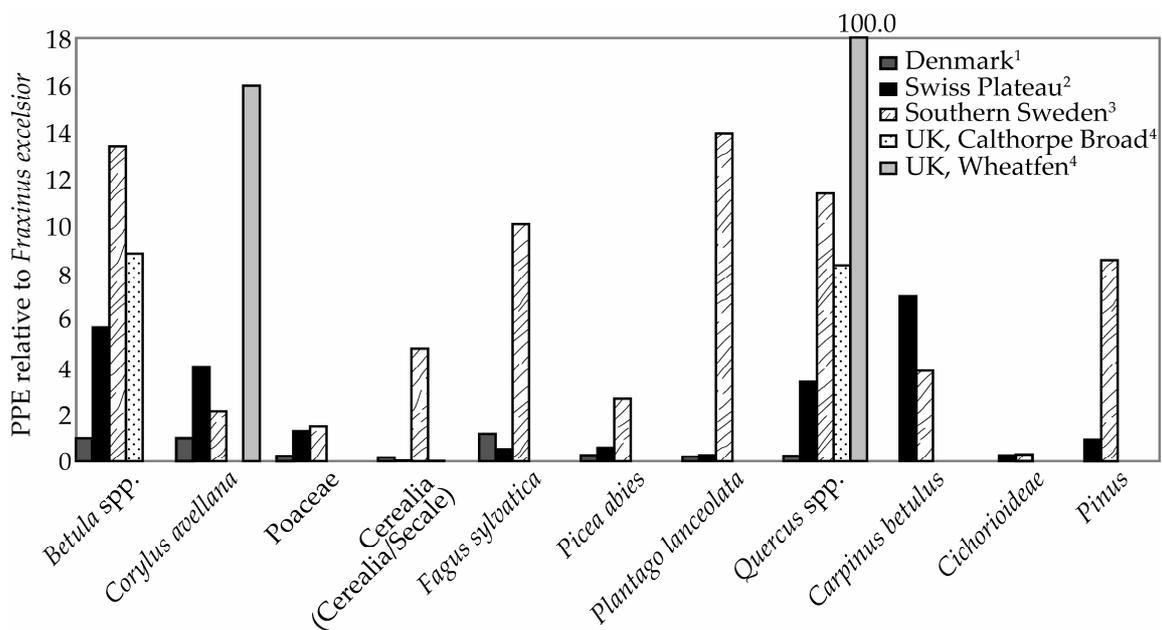


Figure 5 Comparison of the PPE presented in this paper with PPE obtained from previous studies, derived with ERV sub-model 1 and the Prentice-Sugita model. The PPE are relative to *Fraxinus excelsior* (set to 1). Sources: 1, Nielsen (2004); 2, this study; 3, Broström et al. (2004); 4, Bunting et al. (2005). See text for further explanation

In some of the studies not all ERV sub-models were used. We were therefore restricted in our comparison to data derived with sub-model 1. The PPE are expressed relative to *F. excelsior*. Because the PPE were originally expressed relative to grasses, juniper, or oak, they were first recalculated by dividing by the PPE of *F. excelsior* (the PPE of *F. excelsior* becomes 1). Note that the PPE of Denmark are given for the specific taxon, even though they are derived for groups. For instance, *Quercus* was part of a group with *Tilia* and *Ulmus*. *Fraxinus*, *Salix*, *Betula*, and *Corylus* formed another group (Nielsen, 2004).

Cerealia was a combined group of Cerealia-type as well as *Secale cereale* for Denmark and Switzerland, but not for Southern Sweden, where it only comprised Cerealia-type. Different fall speeds were used, so different results are to be expected. *Pinus* is a combination of *P. cembra* and *P. sylvestris* in this study, but for the other studies, it was exclusively *P. sylvestris*.

In general, the PPE reported from Wheatfen (UK) have the highest values, followed by the PPE from Southern Sweden. The high PPE for *Plantago lanceolata* in Sweden is explained by the sampling scheme of the moss polsters that were exclusively taken in open land (Broström et al., 2004). The variance for Cerealia might be explained by the difference in (sub) species in the different regions. However, it is more likely that methodological differences caused the large deviations between the results of small lake and moss polsters.

Broström et al. (2004) suggested influences of sampling design and vegetation survey on the PPE based on a comparison between Norwegian (Hjelle, 1998) and Swedish moss polster pollen data (Broström et al., 2004). They expected large effects of the vegetation survey by cover estimation or presence/absence data. We also expect that scale differences will affect

PPE, since the RSAP of lakes is much larger than that of moss polsters. The vegetation survey areas for moss polsters are much smaller and more manageable than those for lakes are. Furthermore, the vegetation close to the sampling site has major influence on the pollen assemblage, whereas a vegetation survey around a lake might be too general to capture the important shore vegetation. Therefore, the accuracy of PPE from moss polsters is probably higher on smaller spatial scale.

In addition, a temporal aspect may explain differences between pollen sampling methods. For instance, a pollen trap study in the Alps showed that peak years of pollen influx followed years with high summer temperatures for certain taxa, but not for others (van der Knaap *et al.*, 2001). Hicks (2001) advises from similar results in northern boreal forests that when pollen percentages are calculated from moss polsters, the surface sample should at least represent a period of 5 years to avoid extreme variations caused by the climate signal in pollen production. However, when pollen deposition on moss polsters was compared to deposition in pollen traps in Finland, it seems that moss polsters only represent between one to two years of pollen deposition (Räsänen *et al.*, 2004). Lake surface sediments are estimated to represent up to 5 years of pollen deposition, depending on the trophic state and other lake characteristics.

Spatial scale issues are also confirmed by the fact that the PPE for the Swiss Plateau are most similar to those of Denmark, both estimated from small lake data. However, the Danish taxa were amalgamated according to their fall speed and ecology, so that *Fraxinus*, *Betula*, and *Corylus* were part of the same group together with *Salix* and *Alnus*. In the Swedish and Swiss dataset, *F. excelsior* was a lower pollen producer than *Betula* and *Corylus*. The Danish result might have turned out somewhat too low because of the use of *Fraxinus* as reference taxon.

When comparing results from geographically different regions, we should also consider the way in which assumptions of the methods might be strained in the different studies. In the Swiss case, the topography of the landscape may add some uncertainty. Some parts of the Swiss Plateau are hilly, favouring a prevailing wind direction. However, a prevailing wind direction may also occur in other regions.

Although Calcote (1995) found no difference between relative pollen productivity of the same species in two regions in Wisconsin and Michigan (USA), Broström *et al.* (2004) and Bunting *et al.* (2005) observed that PPE varied between subregions in respectively southern Sweden and the UK. In any case, our comparison between the different regions in Europe showed that PPE established for one region were not directly applicable to other regions.

Conclusions

PPE for 13 taxa were obtained for the Swiss Plateau by using surface sediment samples from lakes. Three groups of comparable pollen productivity were found: trees with notably higher pollen productivity than Poaceae, trees with equal or lower pollen productivity than Poaceae and a very low pollen producing group, all being herb taxa. Considering the large standard errors of the PPE of Cerealia, vegetation reconstruction with regard to this taxon could be in-

conclusive in our study region.

The effect of applying different distance-weighting methods to vegetation survey data before using the ERV sub-models is most pronounced for pollen taxa with heavy pollen grains such as *Abies*. For *Abies* PPE are lower when wind speed is increased, and it becomes even lower when inverse distance or inverse squared-distance is applied. It is therefore preferable to use taxon-specific distance-weighting that takes the dispersal characteristics of pollen grains into account.

The Swiss set of PPE differed significantly from those obtained in southern Sweden, Denmark, and the UK. However, it was most similar to the PPE derived from lake samples in Denmark. A comparison between PPE from different regions showed that methodological differences in pollen sampling and vegetation survey may have had an influence on the PPE. Moreover, the variety in pollen productivity between regions indicated that the PPE of one region are not directly applicable to other regions.

CHAPTER 3

EVALUATING SWISS POLLEN PRODUCTIVITY ESTIMATES USING A SIMULATION APPROACH

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*Vegetation History and Archaeobotany*², in press

Abstract

We simulated pollen assemblages for 11 sites on the Swiss Plateau (Schweizer Mittelland) based on a low-resolution land cover map and pollen productivity estimates (PPE) from this region. A comparison between observed and simulated pollen data demonstrated that the majority of the simulated pollen proportions was within a range of 5% of over- or underestimation, and that at eight of the 11 sites the dominant taxon was correctly estimated. The modelled sum of arboreal pollen was correct within $\pm 11\%$ at nine sites. Our results indicate that the PPE established for the Swiss Plateau can be used to simulate pollen assemblages with reasonable accuracy. Moreover, our results justify the use of the POLLSCAPE simulation using the Prentice-Sugita model and its variations of pollen dispersal and deposition in more complex topographic landscapes than those to which they have hitherto been applied.

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Introduction

Quantitative reconstruction of past vegetation requires a better understanding of major mechanisms and factors affecting representation of vegetation from pollen. Theoretical and modelling studies have demonstrated that pollen productivity of individual plant taxa is one of the important factors to relate pollen loading and pollen assemblages in sedimentary basins to the abundance of plants in the surroundings (Prentice, 1985, 1988; Sugita, 1993, 1994). Pollen loading is defined as the pollen input in grains on the surface of a basin (Sugita, 1994). Another critical factor is background pollen, that is pollen loading coming from beyond the “relevant source area of pollen” (*sensu* Sugita, 1994). The pollen-vegetation relationship of individual taxa can differ significantly between regions of different vegetation composition, even when the inter-regional differences in pollen productivity do not exist (Broström *et al.*, 1998; Sugita *et al.*, 1999; Sugita *et al.*, 2006). Therefore, obtaining reliable estimates of pollen productivity and background pollen is a critical step for quantitative reconstruction of vegetation and landscape (Sugita, 2007a, b).

Over the last several years, the number of studies for estimating pollen productivity using the extended R-value (ERV) models (Parsons and Prentice, 1981; Sugita, 1994) has increased in northern Europe (Sugita *et al.*, 1999; Broström *et al.*, 2004; Nielsen, 2004; Bunting *et al.*, 2005; von Stedingk, 2006; Soepboer *et al.*, 2007). Although pollen productivity estimates (PPE) of major plant types are more or less consistent among regions, there are some differences. For example, Soepboer *et al.* (2007) showed that PPE for lowland Switzerland differed from those estimated in other European regions. Differences in sampling strategies and types of sampling sites (moss polsters versus lake surface sediments and different approaches in vegetation survey) may partly explain these differences. Different ERV sub-models also provide slightly different estimates

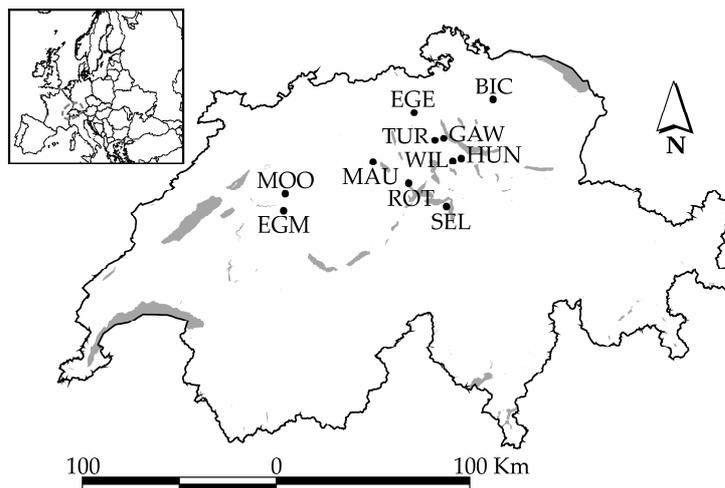


Figure 1 Map of Switzerland with the location of the 11 lakes on the Swiss Plateau used to simulate pollen assemblages. The inset shows the 200 km radius around the Swiss Plateau which was used for estimating regional vegetation abundance (for details, see text)

of pollen productivity because of the differences in model assumptions (Parsons and Prentice, 1981; Sugita, 1994; Broström *et al.*, 2004; Soepboer *et al.*, 2007). Furthermore, pollen productivity may differ between regions because of climate, competition between plant species, different vegetation age, size and genotypes, geology, soil types, or vegetation cover density (Calcote, 1995; Hicks, 2001). These differences in PPE could affect the interpretations of the modern pollen-vegetation relationships (Sugita, 1994; Calcote, 1995; Sugita *et al.*, 1999; Nielsen, 2004;

Bunting and Middleton, 2005) and the reconstruction of past vegetation and landscape using modelling approaches, such as Sugita (2007a; 2007b) and Hellman *et al.* (2007).

This paper attempts to evaluate the effects of the differences in both PPE and background pollen on the pollen-vegetation relationships using the POLLSCAPE simulation (e.g., Sugita, 1994; Sugita *et al.*, 1999; Nielsen, 2004; Bunting and Middleton, 2005; Sugita, 2006). We simulated pollen assemblages using a present-day low-resolution land cover map around 11 lakes selected for this study, estimates of the regional vegetation composition of the Swiss Plateau (Schweizer Mittelland) and its vicinity, and pollen productivity estimates for the Swiss Plateau (Soepboer *et al.*, 2007). The results are compared to the actual pollen assemblages from these sites in order to assess the effects of the differences between the pollen productivity estimates and regional vegetation data on the accuracy of the pollen assemblages simulated by POLLSCAPE.

Study area

The Swiss Plateau is the lowland area roughly between Lake Geneva and Lake Constance (Bodensee), bordered by the Jura Mountains in the northwest and the Alps in the southeast. This region has the highest population density in Switzerland. It is characterized by agriculturally favourable soils and rolling to hilly topography. The area is known for its many lakes of glacial origin, ideal sites for studies of vegetation history (Burga, 1988; Ammann *et al.*, 1996; van der Knaap *et al.*, 2000). In general, pollen diagrams from this region show vegetation changes associated with human impact since the Neolithic and Bronze Age.

Methods and materials

Models and simulations

Pollen assemblages were generated with a program, Polsim.v3.3 (Sugita, unpublished), which includes subroutines for the POLLSCAPE and extended R-value (ERV) models. The POLLSCAPE subroutine is used to simulate pollen assemblages using spatially explicit vegetation data around pollen depositional sites such as lakes, mires and moss polsters (Sugita, 1994; Sugita *et al.*, 1999). Vegetation data can be derived from simulated landscapes (Sugita, 1994; Sugita *et al.*, 1997; Sugita *et al.*, 1999; Bunting *et al.*, 2004; Broström *et al.*, 2005) or from real landscapes (Sugita *et al.*, 1997; Nielsen, 2004). A similar approach was used by Bunting and Middleton (2005) and Caseldine and Fyfe (2006).

The Ring-Source model (Sugita *et al.*, 1999) describes pollen dispersal from a two-dimensional circular source in the landscape and pollen deposition on the entire surface of a circular basin. It is used to calculate distance-weighted plant abundance at a distance from the depositional basin that increases in steps. The model assumes that the dominant transport mechanism of pollen is by wind above the tree canopy (Prentice, 1985, 1988; Sugita, 1993, 1994). The pollen dispersal is based on an atmospheric diffusion model for the release of small particles (Sutton, 1953). Water-borne pollen, wind direction, and height differences between the source plants and depositional basin, as well as topographic features, are not considered in this model. The wind speed is set to 3.0 m s⁻¹. The sensitivity of the model to parameter selection is discussed in recent papers (Bunting *et al.*, 2004; Nielsen, 2004; Nielsen

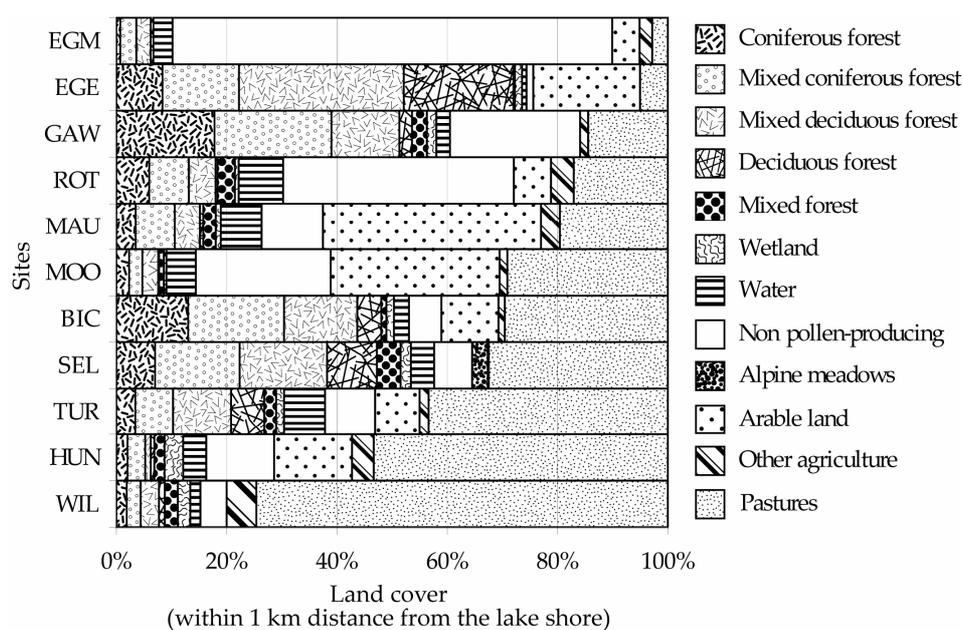


Figure 2 Land cover composition within the 1 km zone around the 11 study lakes

and Sugita, 2005).

Our simulations consider two spatial scales of vegetation and landscape: within the relevant source area of pollen (RSAP) local vegetation, and outside the RSAP regional vegetation. The RSAP starts at the lakeshore and ends at the relevant source distance of pollen (RSDP) that is defined as the distance beyond which additional plant abundance data will not significantly improve pollen-vegetation relationships (Sugita, 1994). In the same phytogeographical region, the pollen loading coming from beyond the RSAP (background pollen) is nearly constant between sites (Sugita, 1994, 2007b). The RSDP on the Swiss Plateau was estimated to be 800 m for small lakes (Soepboer *et al.*, 2007).

Pollen originating from outside the RSAP can be as much as half of the pollen loading in a depositional basin (Sugita, 1994; Calcote, 1995; Soepboer *et al.*, 2007), so including an estimate of regional vegetation will theoretically increase the accuracy of the simulation. One approach to estimate the regional vegetation is to calculate an averaged composition of the small-scale land cover data within 5 km of individual sites. However, in some areas the actual regional vegetation (at a large scale) differs considerably from the vegetation closer to the lakes. This is the case for the Swiss Plateau, which is mostly surrounded by mountain chains. The vegetation at these higher elevations is fundamentally different from that on the Swiss Plateau. We compared two approaches of how a regional vegetation estimate can be derived. The first approach was based on land cover data extending to a distance of 200 km around the Swiss Plateau. In the second approach, the regional vegetation estimate was based on land cover data going out to a distance of 5 km from the lakes studied.

Site selection

The lakes selected for collecting surface samples are all located on the Swiss Plateau (Figure 1), and they are situated in landscapes with different degrees of openness. Figure 2 illustrates the local land cover within the first kilometre around a lake, assuming a RSDP of about 800 m, and that the vegetation within this area is representative of the local vegetation. Surface areas and coordinates of the lakes are given in Table 1. For more information on the lakes and their catchments, see Lotter *et al.* (1997a; 1998).

Table 1 Lake characteristics

Site Name	Abbr.	Height (m asl)	X (Swiss coord.)	Y (Swiss coord.)	Open water area (ha)
Bichelsee	BIC	590	710200	257350	9.2
Egelmösli	EGM	540	602000	199250	2.0
Egelsee	EGE	667	669525	250450	2.3
Gattiker Waldweiher	GAW	545	684750	237050	3.5
Hüttnersee	HUN	658	693750	226600	16.5
Mauensee	MAU	504	648275	224650	60.0
Moossee	MOO	521	602950	207950	31.0
Rotsee	ROT	419	666625	213650	50.0
Seelisberg Seeli	SEL	738	686125	201375	18.3
Türlersee	TUR	643	680275	236025	49.7
Wilersee	WIL	730	689500	225150	3.1

Table 2 Vegetation composition of each land cover class (in %). The total sum need not be 100%, because only 13 species were used in the simulations

	Meadows	Arable land	Coniferous forest	Deciduous forest	Mixed coniferous forest	Mixed deciduous forest	Mixed forest	Non-pollen producing	Other agriculture	Pastures	Water	Wetlands
<i>Abies alba</i>	-	-	19.4	1.0	14.3	6.1	10.2	-	-	-	-	-
<i>Betula</i> spp.	-	-	0.1	1.8	0.6	1.3	0.9	-	-	-	-	15.8
<i>Carpinus betulus</i>	-	-	-	0.7	0.2	0.5	0.4	-	-	-	-	-
Cerealia (sum)	-	53.9	-	-	-	-	-	-	-	-	-	-
Cichorioideae	20.0	-	-	-	-	-	-	-	-	11.9	-	-
<i>Corylus avellana</i>	-	-	-	-	-	-	-	-	-	-	-	2.5
<i>Fagus sylvatica</i>	-	-	3.0	57.3	18.1	42.2	30.1	-	-	-	-	2.5
<i>Fraxinus excelsior</i>	-	-	0.5	9.4	3.0	6.9	5.0	-	-	-	-	3.7
<i>Picea abies</i>	-	-	63.1	3.3	46.5	19.9	33.2	-	-	-	-	5.8
<i>Pinus (sylvestris and cembra)</i>	10.0	-	5.5	0.3	4.1	1.8	2.9	-	-	-	-	11.7
<i>Plantago lanceolata</i>	-	-	-	-	-	-	-	-	-	2.6	-	-
<i>Quercus</i> spp.	-	-	0.4	6.7	2.1	4.9	3.5	-	-	-	-	-
Poaceae	30.0	-	-	-	-	-	-	-	-	41.7	-	39.2

Table 3 Regional vegetation composition within a distance of 200 km, pollen production estimates (PPE) obtained using the three extended R-value (ERV) sub-models (Soepboer et al. 2007) and pollen fall speed

Taxon	Regional composition (%)	PPE1 sub-model 1	PPE2 sub-model 2	PPE3 sub-model 3	Fall speed (m s ⁻¹)
<i>Abies alba</i>	3.83	7.05	6.53	9.92	0.120
<i>Betula</i> spp.	1.85	4.39	4.73	2.42	0.026
<i>Carpinus betulus</i>	0.52	5.40	5.40	4.56	0.042
Cerealia (sum)	22.17	0.10	0.10	0.10	0.078
Cichorioideae	5.47	0.20	0.20	0.17	0.051
<i>Corylus avellana</i>	1.96	3.10	3.05	2.58	0.025
<i>Fagus sylvatica</i>	13.48	0.41	0.54	0.76	0.055
<i>Fraxinus excelsior</i>	4.56	0.77	1.30	1.39	0.022
<i>Picea abies</i>	20.71	0.45	0.35	0.57	0.056
<i>Pinus</i> (<i>sylvestris</i> and <i>cembra</i>)	1.25	0.72	1.76	1.35	0.041
<i>Plantago lanceolata</i>	1.19	0.21	0.09	0.24	0.029
<i>Quercus</i> spp.	3.82	2.60	2.76	2.56	0.035
Poaceae	19.18	1	1	1	0.035

Land use and vegetation

Spatial vegetation data were extracted from a land cover map with a resolution of 100 m using ArcView. This data set is a simplification of the distribution of Swiss land use (1992-1997), provided by the Swiss Federal Statistical Office (GEOSTAT, 1997). We simplified the original classification to the following eight land cover classes: 1) pastures; 2) alpine meadows; 3) arable land; 4) other agriculture; 5) open water; 6) wetlands; 7) non pollen-producing areas (urban areas, glaciers, rock, etc.); and 8) forests. The arable land was distinguished from pastures by overlaying the arable land cover class of the Swiss CORINE land cover data (GEOSTAT, 1998).

Furthermore, the forested areas in the land cover map were subdivided into five classes. We overlaid the original forest class with a 100 m-resolution forest file (GEOSTAT, 1992) which is based on a remote sensing classification of the forests in Switzerland. This resulted in the following five forest classes: 1) coniferous (>90% coniferous trees); 2) deciduous (>90% deciduous trees); 3) mixed forests with a higher proportion of coniferous trees; 4) mixed forests with a higher proportion of deciduous trees; and 5) the remainder of the original forest class that could not be attributed to the other classes, and is defined as mixed forest.

The vegetation composition was compiled for these 12 land cover classes (Table 2), based on previous field surveys (pastures, meadows, and wetlands) or from land use statistics from the Swiss Federal Office of Statistics (arable land). The vegetation composition for forests is based on the Swiss Forest Inventory (Brassel and Brändli, 1999). However, this vegetation composition has to be considered as a rough approximation of the present-day vegetation composition, given that the division between classes (deciduous/coniferous) is not entirely the same as to our land cover map. Land cover abundance at 50 m increments from each lakeshore was calculated out to 5 km using ArcView, and translated into the abundance of

the 13 plant taxa for which Swiss PPE are available (Soepboer *et al.*, 2007).

We compiled and estimated two sets of vegetation composition in the region:

(1) We defined a region as the area within a 200 km zone. It is drawn around a line roughly between Lake Geneva and Lake Constance (Bodensee). The total area includes parts of Germany, France, Italy, Austria and Liechtenstein, as well as Switzerland (see Figure 1). We used a combination of the CORINE land cover database (100 m resolution) as provided by the European Environment Agency (EEA, 2005) as well as the Swiss CORINE land cover file (GEOSTAT, 1998). The Swiss CORINE database contains, however, less detailed forest classifications. To allow a division into mixed, deciduous, and coniferous forests, it was overlain with the 100 m resolution forest file of Switzerland (GEOSTAT, 1992). Species composition within the regional land cover classes was mostly based on field surveys on the Swiss Plateau. The percentage of cereals in arable land was estimated from Swiss land use statistics. The resulting regional vegetation composition is given in Table 3.

(2) Another set of vegetation composition data in the region was defined and calculated as follows: we first compiled vegetation and land cover data within 5 km of each of the 11 lakes and calculated the vegetation composition around each site. The regional estimate of vegetation composition as the percentage cover of the 13 plant taxa was then calculated as the average of the 11 estimates of the vegetation composition.

These two sets of the regional vegetation composition data are not identical. The two data sets were fed into Polsim v3.3, the program used for simulations, in order to evaluate which would be more appropriate to use for studying the pollen-vegetation relationships.

Pollen data

In 1993 and 1994 surface sediments were collected with a gravity corer from either the centre or the deepest part of the lakes (Lotter *et al.*, 1997a; van der Knaap and van Leeuwen, 1998). The top-1 cm of sediment was treated with conventional palynological methods (van der Knaap *et al.*, 2000) and analyzed by the same person (J.F.N. van Leeuwen).

Pollen productivity estimates (PPE)

Pollen-vegetation relationships can be established using three sub-models of the ERV-model (Parsons and Prentice, 1981; Sugita, 1994). The sub-models differ in the way the background pollen component is defined. Three sets of PPE were obtained using pollen data from 20 small lakes and vegetation data going out to 1 km from the lake basin on the Swiss Plateau, using ERV sub-models 1, 2, and 3 (Soepboer *et al.*, 2007). To account for small variations in PPE at distances greater than 800 m (the RSDP in the region), the PPE between 810 and 980 m from the lakeshore were averaged and used here. The average radius of the twenty small lakes used was 190 m. Table 3 provides PPE and taxon-specific fall speed of pollen (pollen precipitation rate). In the table, PPE1 represent pollen productivity estimates using ERV sub-model 1, PPE2 using ERV sub-model 2, and PPE3 using ERV sub-model 3. Soepboer *et al.* (2007) provides detailed description of the methods and parameter values used for data analysis. In addition, since the original PPE for Cerealia were extremely low, we set them arbitrarily to 0.1 for all sub-models to allow for sensible model output. Nevertheless, this still represents one of the lowest values within the whole dataset.

Results

Figure 3 shows the simulated and observed pollen assemblages for all sites, using a regional vegetation estimate derived from the CORINE dataset extending to 200 km from the Swiss Plateau. Poaceae are correctly simulated as the dominant taxon at nine sites. Overall, they are overestimated, but still reasonably close to the observed values. The percentages of simulated arboreal pollen (AP) are slightly underestimated compared to the observed AP percentages.

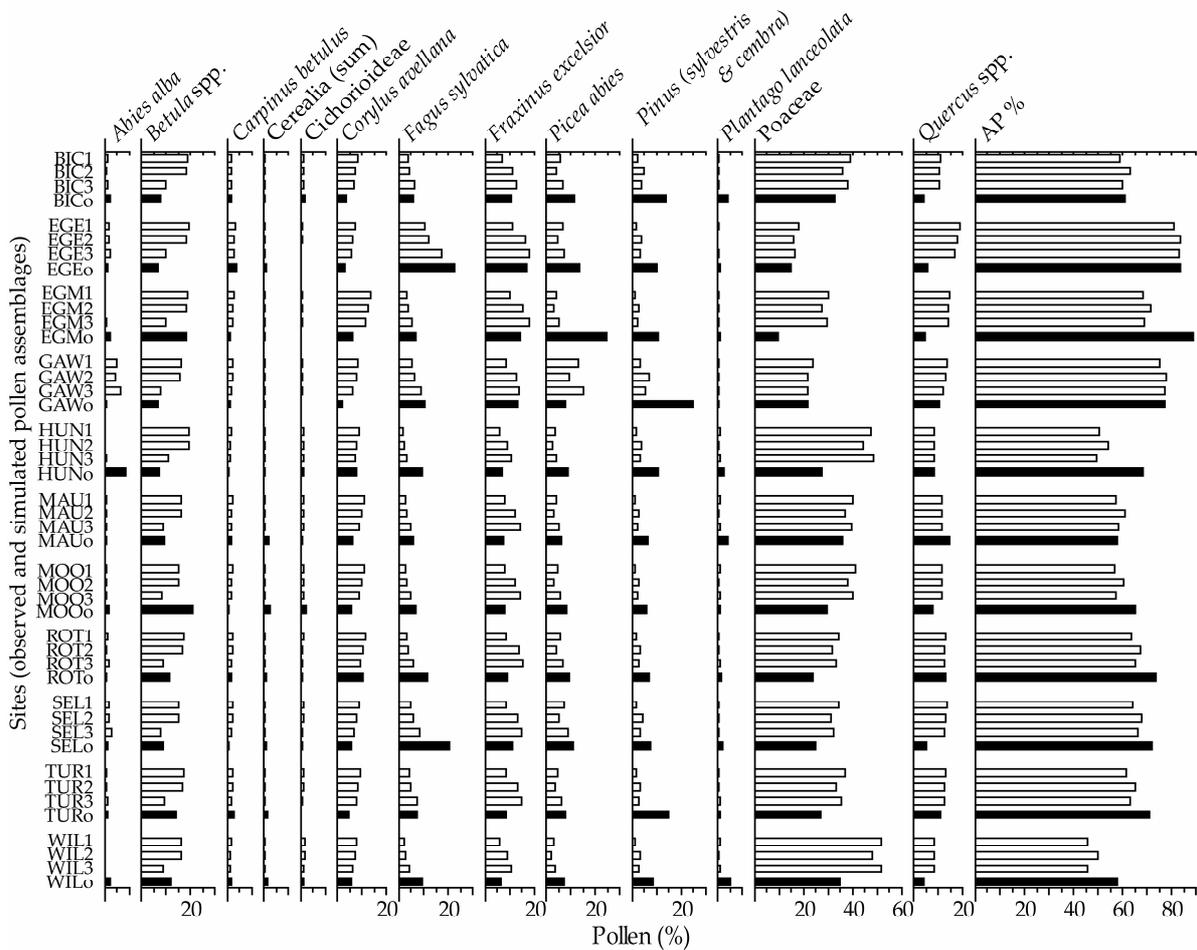


Figure 3 Simulated and observed pollen assemblages for 11 sites on the Swiss Plateau, using three sets of pollen productivity estimates (PPE) calculated with extended R-value (ERV) sub-model 1, 2, and 3. A regional vegetation estimate derived from land cover data going out to a distance of 200 km was used. The simulated pollen assemblages are shown in white, the observed pollen assemblages in black. The number following the abbreviated name of a site (1 to 3) refers to the set of PPE used, whereas 'o' refers to the observed value

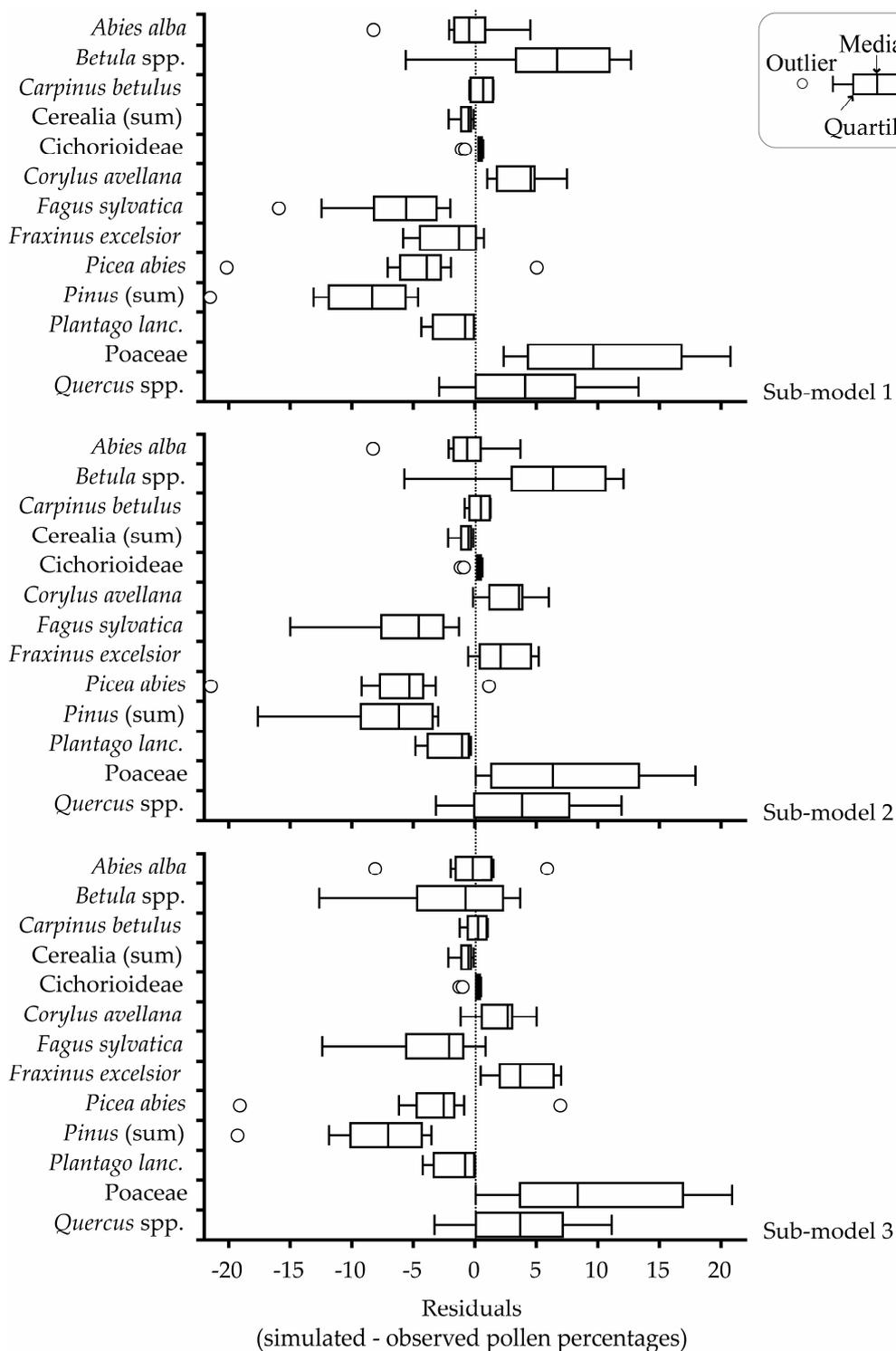


Figure 4 Residuals of simulated versus observed pollen percentages per taxon for 11 sites. A positive residual value signifies that the simulated pollen percentage is overestimated with respect to the observed value. Each box represents 50% of the data with the median value displayed as a line. The lines extending from the sides of the box mark the minimum and maximum values within the data set that fall within an acceptable range. Any value outside of this range (circle) is considered an outlier

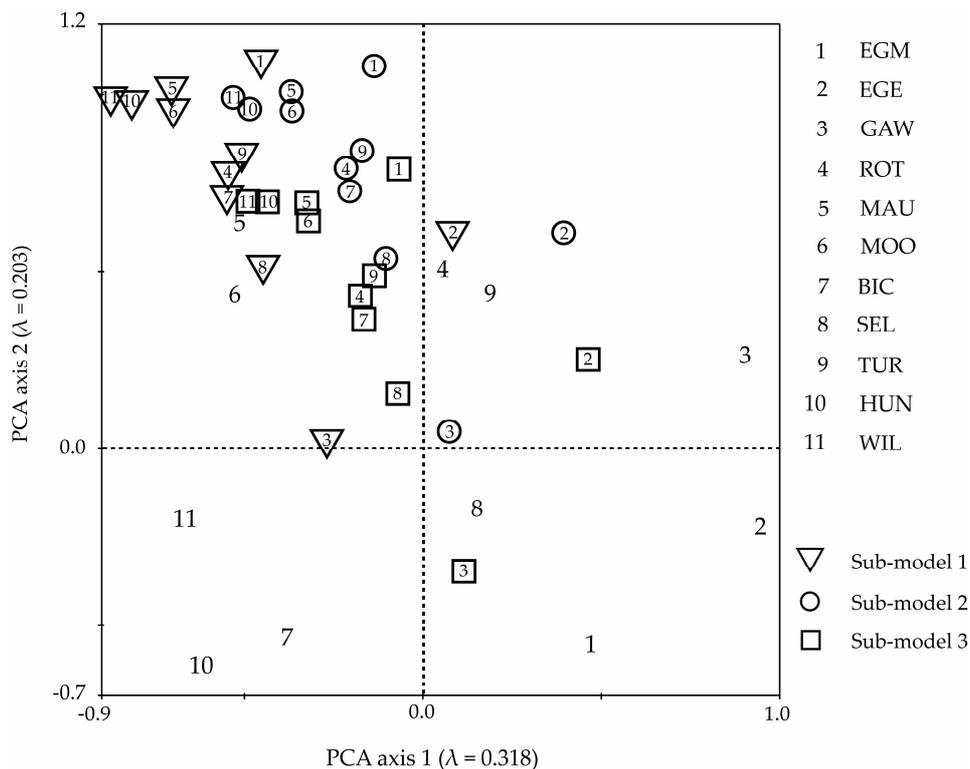


Figure 5 Principal Component Analysis of observed pollen assemblages showing the first two PCA axes, with simulated assemblages used as passive samples

To visualize the accuracy of the simulated pollen proportions relative to the observed pollen proportions for individual taxa, the distribution of the residuals of the pollen proportions is shown in Figure 4. Positive values indicate an overestimate of a taxon in the simulated pollen assemblages, whereas negative values signify an underestimate.

Clearly, Poaceae are overestimated at all sites, regardless of the selection of PPE. To a lesser extent *Corylus* and *Quercus* are also overestimated at most sites. *Fagus*, *Pinus*, and *Plantago* are always underestimated. *Fraxinus* is mostly underestimated when using PPE1, but overestimated using PPE2 and PPE3. *Betula* is generally overestimated using PPE1 and PPE2.

The median values for *Abies*, *Carpinus*, *Cerealia*, *Cichorioideae*, *Corylus*, *Fagus*, *Fraxinus*, *Plantago*, and *Quercus* are within a range of $\pm 5\%$ of the observed values. This is also true for *Betula* using PPE3, *Fagus* using PPE2 and PPE3, and *Picea* using PPE1 and PPE3. The values are somewhat higher for *Betula* using PPE1 and PPE2 ($\sim 6.5\%$), for *Fagus* using PPE1 (-5.5%), and for *Picea* using PPE2 (-5.3%). The medians of Poaceae are between 6.4 and 9.7% and those of *Pinus* between -6.1 and -8.3% .

The ranges shown in Figure 4 can be large for some taxa, indicating that the degrees of dissimilarity between modelled and observed values vary between sites. This is true for *Betula*, *Fagus*, *Pinus*, Poaceae, and *Quercus*. The ranges and outliers demonstrate that the largest difference between simulated and observed pollen proportions is slightly over 20%.

Figure 5 shows the result of a principal component analysis (PCA), using CANOCO 4.5 (ter Braak and Šmilauer, 2002), of the observed pollen assemblages from 11 sites and the simulated pollen assemblages at the sites using POLLSCAPE with three different sets of PPE. The percentage data were log-transformed and the simulated data were used as passive samples in the PCA. The distance between the different samples represents the dissimilarity of their species composition as measured by their Euclidian distance. The PCA results show that the pollen assemblages simulated using PPE3 are most similar to the observed assemblages, followed by those simulated using PPE2. The highest dissimilarity occurs when PPE1 is applied. However, the model results are generally closer to each other than they are to the observed values.

When the composition of the regional vegetation estimated from the eleven areas with a 5-km distance was used, the dissimilarities between the simulated and observed pollen percentages are generally larger (Figure 6) than those in Figure 3. For example, this is true for the simulated and observed total AP-percentages. Poaceae are highly overestimated in the simulations at all sites, except at Mauensee (MAU) (Figure 6).

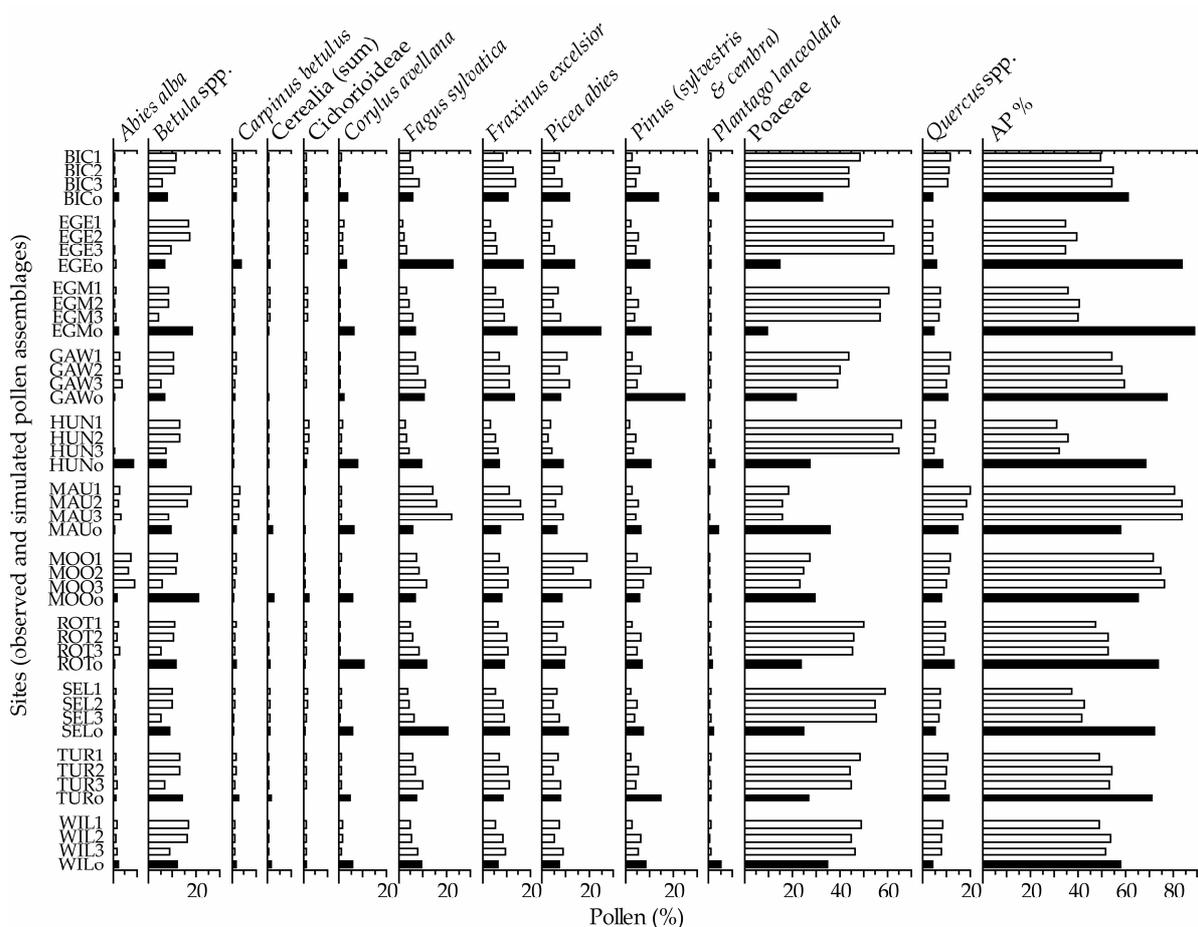


Figure 6 Simulated and observed pollen assemblages for 11 sites on the Swiss Plateau, using three sets of PPE calculated with ERV sub-models 1, 2, and 3. A regional vegetation estimate derived from averaged local vegetation going out to a distance of 5 km was used; see also Figure 3

Discussion and conclusions

Our results showed that the simulation output (modelled with a regional vegetation component going out to 200 km from the Swiss Plateau) reproduced the general trends in the observed pollen assemblages from the 11 lakes. Except for Poaceae and *Pinus*, the median of the range of under- or overestimation was close to or within a range of 5%. At the eight sites among the 11, the dominant taxon was correctly estimated. Allowing for a range of 11% difference between observed and simulated values, the AP percentages were accurately estimated at nine sites, whereas at two sites the difference was of about 20%.

Several factors should be considered to explain the discrepancies between the observed and simulated pollen assemblages; these include boundary conditions of the model (wind speed, type of regional vegetation estimate, extent of regional vegetation, lake radii), the representation of the spatial resolution of vegetation patterns and classification (grid size, number of classes), the patch size of vegetation classes in the vegetation, the number of taxa, the occurrence and distribution of rare taxa, and last but not least the differences in pollen productivity estimates (Sugita, 1994; Sugita *et al.*, 1999; Bunting *et al.*, 2004; Nielsen, 2004). Furthermore, pollen percentages are closed compositional data, so an overestimation of one taxon directly results in an underestimation of one or several other taxa. The reasons for the discrepancies may, therefore, be complex.

Vegetation along the lakeshores might have a large influence on pollen assemblages, yet it is difficult to include using low-resolution land cover data. Nevertheless, of the three potential shoreline taxa used in our dataset (Poaceae, *Betula* and *Fraxinus*), only *Fraxinus* was slightly underestimated. Therefore, the effect of low-resolution land cover data on the representation of shoreline vegetation seems minimal in this study. The effect might increase if plants indicative of wetlands, such as Cyperaceae, *Salix*, *Alnus*, or *Populus* were included in data analyses and simulations.

The accuracy of simulation results varied from site to site. A reason could be that the use of averaged taxon distribution per land cover class caused smoothing of the calculated taxon abundance, so less extreme vegetation proportions were estimated than might actually be encountered in the field. This may have happened at Hüttnersee (HUN) and Seelisberg Seeli (SEL), where far more *Abies* or *Fagus* pollen were observed than estimated. The influence of taxa composition and specific land cover around a site is clearly visible at Egelmöslü (EGM), located within the city of Bern. This site showed the highest dissimilarities between simulated and observed values. Simulated values especially for Poaceae and *Pinus* are off by 20%. About 80% of the surrounding land at Egelmöslü consists of the non pollen-producing land cover class (Figure 2). This implies that local vegetation estimates are based on about 20% of the surrounding area, which increases statistical uncertainty. Still, at most sites the models accurately estimate the dominant pollen taxon and the landscape openness (AP/NAP ratio) around a site, provided that the regional vegetation estimate is based on a very large area.

Among the different estimates of pollen productivity used in the simulations, PPE3 provided the simulated percentages that were closest to the observed values. This was also confirmed

by the PCA results (Figure 5). In particular, the *Betula* proportions obtained with PPE3 (2.5) were closer to the observed ones than those obtained with PPE1 and PPE2 (~4.5). The slightly higher values for *Fraxinus* and *Picea* in the set of PPE3 also slightly improved the simulation results.

We expected a strong influence of regional vegetation composition upon the simulated pollen assemblages. As up to half of the pollen in a sample may originate from regional vegetation (Soepboer *et al.*, 2007), an accurate estimate for this regional vegetation composition is paramount. We estimated regional vegetation by using a land cover map on the European scale. However, taxa abundance estimates within the regional land cover classes were based on field surveys on the Swiss Plateau. One of the most consistent discrepancies between the simulated and observed pollen proportions can be attributed to this small-scale field survey, which may imply an underestimation of *Pinus* (*P. cembra* and *P. sylvestris* pollen type, which includes also *P. mugo*) in the vegetation data and, therefore, an underestimation of *Pinus* in the simulated pollen assemblages. In Switzerland, most *Pinus* grows at higher elevations in the subalpine zone, which were not included in the vegetation surveys of the Swiss Plateau. Therefore, the amount of *Pinus* should probably be higher in the regional vegetation composition. A higher simulated pollen proportion for *Pinus* could, in turn, lower the overestimation of Poaceae.

To assess the effect of regional vegetation on pollen loading, a regional vegetation estimate based on the average vegetation abundance up to 5 km from the lakeshores was also used for an additional simulation experiment (Figure 6). In this case, the simulated Poaceae percentages were considerably overestimated compared to the observed proportions. Both this additional experiment with averaged small-scale vegetation data used as regional vegetation, as well as the underestimation of *Pinus*, demonstrate that reliable estimates of the regional vegetation composition are critical and necessary to increase the accuracy of the POLLSCAPE simulation. It is advisable to use regional vegetation estimates from a very large area to increase the reliability of the simulation results.

The current version of the POLLSCAPE simulation model included in Polsim.v3.3 does not take into account the topographic complexity of the Swiss Plateau, prevalent and changing wind directions, effects of orographic wind, or differences in source height of pollen between trees and herbs. However, despite the simplicity of the model, the results suggested that the PPE for the Swiss Plateau (Soepboer *et al.*, 2007) are within an acceptable range of accuracy. In addition, this study justifies the use of simple model-based reconstruction methods based on the Prentice-Sugita approach in regions where topographic conditions are more complex than in the regions where these methods have hitherto been applied, such as North America, the British Isles, or Scandinavia (Sugita, 1994; Calcote, 1995; Sugita *et al.*, 1999; Broström, 2002; Nielsen, 2004; Broström *et al.*, 2005; Bunting *et al.*, 2005; Nielsen and Odgaard, 2005; Nielsen and Sugita, 2005).

CHAPTER 4

ESTIMATING PAST VEGETATION OPENNESS BY POLLEN-VEGETATION RELATIONSHIPS: A MODELLING APPROACH

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Abstract

We used a modelling approach to assess past landscape openness in mid-Holocene natural vegetation. Two simple landscape scenarios were modelled: a first landscape was based on the “Vera cycle” hypothesis, including different phases of herbivore-induced vegetation change and regeneration, while a second landscape was based on potential mid-Holocene natural vegetation on the Swiss Plateau following the closed canopy theory. Using a pollen dispersal and deposition model, these simulated landscapes were used to produce pollen assemblages. The resulting modelled pollen assemblages were then compared to a typical mid-Holocene pollen record from the Swiss Plateau. Our results indicated that the mid-Holocene pollen record is likely to be the result of a closed beech forest. However, the vegetation cover on the Swiss Plateau had components from both the closed woodland and wood pasture landscape designs. The later probably at frequently disturbed or naturally open habitats.

Introduction

The management of near-natural forest ecosystems in Europe has been under debate during the last decades. Generally, it is assumed that in temperate climates the zonal vegetation succession leads to a climax vegetation consisting of closed canopy forest (e.g., Ellenberg, 1982; Burga and Perret, 1998) in which regeneration of trees takes place in small gaps. This idea has been generally supported by palynological data from Central and North-western Europe (e.g., Berglund *et al.*, 1996), suggesting that lowland landscapes on nutrient-rich, humid soils were mainly covered by dense woodland vegetation during the Holocene and previous interglacials. However, Vera (2000) and others interpreted the high abundance of *Quercus* and *Corylus* in European Holocene pollen assemblages as reflecting an open to semi-open park-like landscape rather than closed canopy forests, because these species are not able to regenerate in shady circumstances. Large herbivores are thought to have maintained a park-like open landscape, already before the onset of anthropogenic forest clearance. These open landscapes were comparable to the wood pastures that were established in Europe during Medieval times. Mitchell (2005) simplified the crux of the problem as follows: the traditional view implies that forest structure dictates herbivore density, whereas the Vera hypothesis says that herbivore density controls forest structure.

Vera (2000) distinguishes different phases of vegetation development starting with the development of thorny bush in open grassland in which seedlings of trees can grow sheltered from large herbivores, like bison and deer. Eventually, the crowns of the trees grow out of the bushes and by growing together they are forming a grove. The grove can extend when the bushes expand further into the grasslands. Within the grove, regeneration of trees is not possible because of shady conditions and browsing and trampling of the large herbivores. Opening up of the grove is possible when the herbivores strip the trees, or by natural catastrophes like droughts, storms, fires, flooding, and diseases. When increasingly large areas turn into open terrain, the grove will turn into grassland again, because of foraging of the large herbivores. Thorny shrubs eventually establish themselves and the process repeats. Kirby (2004) modelled this cycle by using different landscape structures to mimic land cover change for a 2500 ha area over a 500-year period. One of the landscapes, a predominantly wooded landscape with half of it as a woodland phase, a quarter as a park phase, 15% as a scrub, and 10% as a break-up phase, was compatible with the assumptions that define a herbivore-driven dynamic process: only with these settings, open landscape and old trees could maintain over time and space (Kirby, 2004).

Several authors have used palynology to waylay the wood pasture theory that Vera (2000) proposed. Svenning (2002) used the percentage non-arboreal pollen from the last interglacial and from the pre-agricultural Holocene, when human impact was negligible, to indicate vegetation openness in four different major landscape units. He concluded that closed forest predominated, but that longer-lasting openings could have occurred. In addition, open vegetation would have been frequent on floodplains, nutrient-poor soils, and in dry and warm areas, where large herbivores and fire were key forcing factors for vegetation. Mitchell (2005) compared Holocene pollen assemblages from mainland Europe with Irish pollen assemblages at a time when large herbivores were already extinct in Ireland. Based on the similar-

ity between the datasets he concluded that large herbivores could not have been driving the abundance of *Quercus* and *Corylus*. Moreover, Mitchell (2005) concluded from the comparison of small-scale pollen data of European and North-American sites that an open canopy forest could only maintain when human exploitation of such a forest had started. Nevertheless, large herbivores could influence the species compositions in the forests.

Bradshaw *et al.* (2003) argued that the closed forest theory was not a perfect model for the early Holocene vegetation structure alone, because it could not explain the long-term maintenance of *Quercus* and *Corylus* in the pollen records. He proposed a forest consensus theory, in which closed canopy forest is indeed the climax vegetation during interglacials. Because of many disturbances such as floods, fires, or wind-throw, and locally by animals such as beavers and deer, some parts of the landscape may remain open. Fire together with grazing pressure of herbivores may have created appropriate conditions for regeneration of *Quercus*, *Corylus* and *Pinus* without the development of so-called 'wood pastures'. Soil properties and pedogenesis are also responsible for variations in the vegetation composition. For instance, sandy soils are less fertile and have lower water retention than loamy soils and would give forests more open in structure. In such open vegetation, *Quercus* and *Corylus* prosper as light-requiring species, and pine as a more fire tolerant tree. These factors created a varied landscape with a high diversity (Bradshaw *et al.*, 2003).

The above-mentioned hypotheses are strongly based on the results of pollen analyses. Often non-arboreal pollen (NAP) percentages are used to estimate vegetation openness, however, this method is in practice and in theory not accurate (Broström *et al.*, 1998; Sugita *et al.*, 1999). Model-based reconstructions of regional vegetation in the Holocene have shown that pollen proportions underestimate landscape openness (Sugita *et al.*, 2007).

The interpretation of pollen data is complex because of differences in pollen production, dispersal, and deposition among plant taxa (Parsons and Prentice, 1981; Prentice and Parsons, 1983; Prentice, 1985; Sugita, 1993, 1994). For instance, for some regions in Europe it is estimated that *Quercus* and *Corylus* produce more pollen per surface area than *Fagus* (e.g., see the comparison in Soepboer *et al.*, 2007). Also, the pollen grains of these two taxa are more suitable for dispersal (Eisenhut, 1961; Gregory, 1973), leading to a higher amount of their pollen in the pollen assemblages and thus to higher pollen percentages relative to other species.

The taxon-specific characteristics of pollen productivity and dispersal are used in the Extended R-value (ERV) models (Parsons and Prentice, 1981; Prentice and Parsons, 1983; Prentice, 1985, 1988; Sugita, 1993, 1994) that describe pollen-vegetation relationships. When vegetation abundance around small to medium-sized lakes is surveyed and distance-weighted taking the dispersal characteristics of the pollen into account (Prentice, 1985, 1988; Sugita, 1994), the ERV models provide, amongst others, Pollen Productivity Estimates (PPE) and a measure for the relevant source area of pollen (Sugita, 1994). Recently, such PPE have been established for several regions (Sugita, 1994; Calcote, 1995; Jackson and Kearsley, 1998; Sugita *et al.*, 1999; Broström *et al.*, 2004; Nielsen, 2004; Bunting *et al.*, 2005; Soepboer *et al.*, 2007). Moreover, the ERV models allow testing of the effect of changing vegetation and species

composition and distribution on pollen assemblages. At the same time it is possible to run multiple past landscape scenarios that can be evaluated by fossil pollen assemblages (Sugita, 1994; Sugita *et al.*, 1999; Eklöf *et al.*, 2004; Middleton and Bunting, 2004; Bunting and Middleton, 2005).

In this study, we used a modelling approach to assess past landscape scenarios using data from the Swiss Plateau. Two landscape designs mimicked two scenarios of a mid-Holocene landscape in lowland Switzerland. The first landscape was based on the Vera cycle with different vegetation phases as described by Kirby (2004) to be compatible with herbivore-driven processes, whereas the second was based on potential natural mid-Holocene vegetation for the Swiss Plateau following the closed canopy theory. The resulting simulated pollen assemblages for small lakes were then compared to a typical mid-Holocene pollen record from the Swiss Plateau.

Material and Methods

POLLSCAPE

POLLSCAPE is a modelling scheme for pollen dispersal and deposition (Sugita, 1994; Sugita *et al.*, 1997; Sugita *et al.*, 1999) in which vegetation abundance data can be distance weighted by the Prentice-Sugita model (Prentice, 1985, 1988; Sugita, 1993) to correct for differences in pollen production and dispersal between species. This sub-routine is incorporated in the software POLSIM, which also includes ERV sub-models (Parsons and Prentice, 1981; Prentice and Parsons, 1983; Sugita, 1994). A linear relation is assumed between pollen loading [e.g., grain m⁻²] in a sedimentary basin and vegetation abundance [e.g., kg m⁻²] surrounding the basin. The slope and intercept of the pollen-vegetation relationship are pollen productivity and a background pollen component.

When the vegetation survey area is increased, the distance-weighted vegetation abundance becomes nearly constant at a certain distance for the basins. The area out to this distance is defined as the Relevant Source Area of Pollen or RSAP (Sugita, 1994). The RSAP can be derived from the 'likelihood function scores', in which the ERV-models measure the goodness-of-fit of the pollen-vegetation relationship based on the maximum likelihood method. The graph plotting the maximum likelihood scores with increasing distance from the lakeshore will in principle reach an asymptote at a certain distance. This is the RSAP (Sugita, 1994). The vegetation inside the RSAP produces a local pollen component, whereas the vegetation outside the RSAP produces the regional pollen component (Sugita, 1994). The RSAP has been determined from field data at the Swiss Plateau to be the area out to 800 m from the lakeshores of small to medium-sized lakes (Soepboer *et al.*, 2007).

Table 1 Pollen Productivity Estimates (PPE) and pollen fall speed

<i>Taxon</i>	PPE	Fall speed (m s ⁻¹)
<i>Betula</i> spp.	2.42	0.026
Cichorioideae	0.17	0.051
<i>Corylus avellana</i>	2.58	0.025
<i>Fagus sylvatica</i>	0.76	0.055
<i>Fraxinus excelsior</i>	1.39	0.022
<i>Plantago lanceolata</i>	0.24	0.029
Poaceae	1	0.035
<i>Quercus</i> spp.	2.56	0.035
<i>Pinus (cembra & sylvestris)</i>	1.35	0.041
<i>Abies alba</i>	9.92	0.120

Three methods have been used to apply the theory behind POLLSCAPE: 1. MOSAIC (Middleton and Bunting, 2004) that allows landscape design; 2. OPENLAND (Eklöf *et al.*, 2004), that classifies vegetation in stepwise increasing distances from the sampling sites; and 3. POLSIM (Sugita, 1994; Sugita *et al.*, 1997), that estimates the pollen input on the surface of a basin (pollen loading). Pollen fall speed (i.e., velocity of deposition, m s^{-1}), PPE for individual taxa, as well as vegetation maps and the location and size of the depositional basins are needed as input parameters for these models. The PPE and pollen fall speeds used here (Table 1) refer to Soepboer *et al.* (2007). The PPE were derived from modern pollen and vegetation data on the Swiss Plateau, using ERV sub-model 3 (Sugita, 1994). Wind speed in the simulations was set to 3 m s^{-1} .

Landscape design

The artificial landscape used for modelling was inspired by the wood pasture as described by Kirby (2004). It was designed in such a way that it allows an herbivore-driven dynamic process, i.e. the forest cycle as proposed by Vera (2000). In this landscape open conditions as well as old groves co-exist, creating a mosaic of habitats at a scale of a few hundred metres (Kirby, 2004). A quarter of the landscape is in a park-like state (park phase, i.e. open with some scattered trees). Half of the landscape is forested (woodland), and the remaining 25% consist of different intermediate phases between open and forested (shrub and break-up stand) vegetation.

We created landscapes of $10 \times 10 \text{ km}$ with a resolution of 10 m . The cell size should be sufficiently small to allow reasonable measurements of RSAP (Bunting *et al.*, 2004), while the radii of the vegetation patches should be equal or larger than the lake radii. The landscape has a matrix of the vegetation type shrub. Then, circular patches (600 m radius) of woodland, and subsequently smaller circular patches (400 m radius) of park and small patches (200 m radius) of break-up stands were randomly placed within the landscape. Eventually, a lake was placed in the centre of the landscape (200 m radius), surrounded by a fringe (10 m width) of shore vegetation. In this way, 20 unique wood pasture landscapes were created (20 lakes). The distribution of the vegetation types became 16.0% (st.dev. ± 1.1) for shrub, 27.0% (± 0.4) for the park phase, 46.9% (± 1.1) for woodland and 10% (± 0.0) for the break-up phase. The area of water was 0.1% and the area of shore vegetation was less than 0.1% .

For the closed forest, only three of the above-mentioned vegetation units were used. The landscape was first filled with woodland. Then small patches (200 m radius) of break-up stands were randomly placed. Similar to the wood pasture landscapes, a lake with a 200 m radius with a fringe of shore vegetation around it was placed in the centre of the landscapes. The distribution of the vegetation types was 89.9% for woodland (± 0.0) and 10% (± 0.1) for the break-up phase. The area cover of water and shore vegetation was similar to the wood pasture landscapes. Figure 1 shows an example of each landscape design.

The simulated pollen assemblages were compared to a mean (three samples) pollen assemblage representing ca. 6000 cal. BP from Lobsigensee (Ammann, 1989). This is a small lake on the Swiss Plateau at 520 m asl with a typical mid-Holocene pollen stratigraphy.

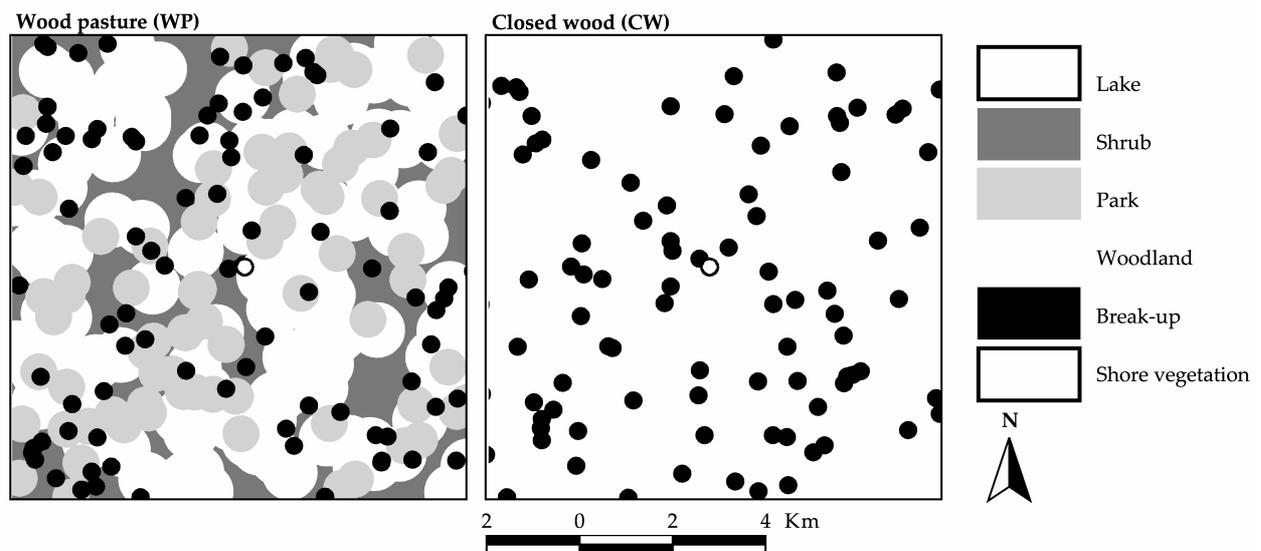


Figure 1 Examples for a wood pasture and a closed woodland landscape as used in the simulations. The 10 m wide fringe of the lakes consist of shore vegetation (hardly visible at this scale)

Vegetation composition

Vera (2000) has indicated taxa that are representative of grassland and vegetation that forms the transition between grassland and woodland, such as Umbelliferae, *Urtica*, *Prunus*, *Crateagus*, *Viburnum*, *Corylus*, etc. Most of these taxa are insect-pollinated and, therefore, often scarce in pollen assemblages. In addition, estimates of pollen fall speed are not available for all taxa. Therefore, only *Corylus* was included in our models.

We used only the taxa for which PPE are available from the Swiss Plateau and that were present in representative pollen diagrams during the mid-Holocene (Ammann *et al.*, 1996). As period of comparison, we chose 6000 cal. years BP because at this time human impact is generally low and local. Moreover, most of the key climax trees (e.g., *Fagus*, *Abies*) had arrived on the Swiss Plateau and were playing a major part in the pollen diagrams (Ammann *et al.*, 1996). *Carpinus* and *Picea* had not yet migrated into the Swiss Plateau from their glacial refugia. According to Burga and Perret (1998), the dominant climax vegetation (i.e., without human impact) in Switzerland would be *Quercus* or *Quercus-Carpinus betulus* forest below 600 m asl, whereas in the submontane belt *Fagus sylvatica* would be dominant. In the montane and subalpine belt more coniferous trees such as *Abies alba* and *Pinus (sylvatica and cembra)* are found. At waterlogged areas, specialised azonal vegetation is present.

The composition of the shore vegetation was derived from the average shore vegetation that was surveyed around 20 small lakes on the Swiss Plateau in 2003 (Soepboer *et al.*, 2007). For the park vegetation, we set a high Poaceae content, with some scattered trees still present. As bushes develop (shrub phase) trees can grow in places that are sheltered from browsing and grazing herbivores. Then, woodland develops with a more or less closed canopy. Here, no herbs are present. For woodland, we used 4 different vegetation compositions that mostly differ in the amount of *Fagus* and *Quercus*. After the woodland begins to break up, the amount of open landscape increases, represented by increasing Poaceae cover.

Table 2 Vegetation composition (%) per vegetation class

	Shore	Park	Shrub	Break-up	Wood-land 1	Wood-land 2	Wood-land 3	Wood-land 4	Regional
<i>Betula</i> spp.	20	5	10	3	0	0	0	0	0
Cichorioideae	3	9	7	7	0	0	0	0	0
<i>Corylus avellana</i>	10	5	33	2	0	0	0	0	5
<i>Fagus sylvatica</i>	1	3	4	35	60	70	80	90	30
<i>Fraxinus excelsior</i>	15	5	1	5	10	10	10	5	0
<i>Plantago lanceolata</i>	0	10	8	8	0	0	0	0	0
Poaceae	40	60	30	30	0	0	0	0	20
<i>Quercus</i> spp.	10	3	7	10	30	20	10	5	10
<i>Pinus (cembra & sylv.)</i>	1	0	0	0	0	0	0	0	10
<i>Abies alba</i>	0	0	0	0	0	0	0	0	25

The share of pollen originating from regional vegetation in modern lake surface sediment samples on the Swiss Plateau is about 50% (Soepboer *et al.*, 2007) and needs to be included to secure accurate simulations (Soepboer *et al.*, in press). Therefore, we also included regional vegetation composition in the modelling. In this way, the influence of a larger landscape surrounding the 10x10 km plots is considered. The regional vegetation composition was based on the composition of climax vegetation in different altitudinal belts in Switzerland and the proportion of area covered by these elevation classes. We used the same regional vegetation for the wood pasture simulations. The vegetation composition of all classes is shown in Table 2. The resulting pollen assemblages are named after the different woodland compositions designs: CW1 to 4 (closed wood) and WP1 to 4 (wood pasture).

Results

RSAP

In Figure 2 the results are shown of the likelihood function scores, which measure the goodness-of-fit of the pollen-vegetation relationship in POLSIM. The RSAP is determined at the distance where the likelihood function scores reach an asymptote. For the closed wood scenarios, these graphs reached asymptotic values between 1000 and 1500 m from the lakeshore. The wood pasture scenarios showed longer tails; there the RSAP were reached between 1500 and 2000 m.

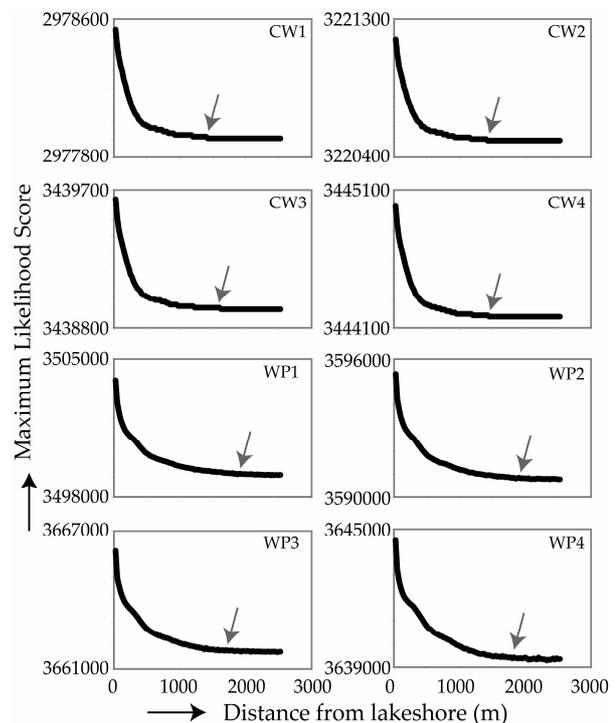


Figure 2 Likelihood function score graphs with arrow indicating the radius of the relevant source area of pollen

Pollen assemblages

Figure 3 shows the simulated pollen assemblages for all eight scenarios. In general, the relative amount of herbaceous and shrub taxa was higher in the wood pasture assemblages, whereas the tree taxa were more abundant in the “closed wood” assemblages.

With the differences in the woodland compositions (1 to 4, see Table 2), we mainly see effects on the species whose cover increased in composition 1 to 4 (*Fagus*) or decreased (*Quercus* and in woodland 4 also *Fraxinus*). In CW1 to 4, *Fagus* proportions increased from 15 to 31%, while *Quercus* proportions decreased from 52 to 26%. In WP1 to 4, *Fagus* proportions increased from 9 to 14% and *Quercus* proportions decreased from 32 to 19%. However, we also see that *Corylus*, *Poaceae*, *Pinus* as well as *Fraxinus* increased from CW1 to 3. *Fraxinus* decreased in the scenarios CW4 and WP4 compared to CW3 and WP3, respectively.

The pollen assemblages of CW2 and WP2 can be roughly taken as the averaged results of the two conflicting landscape designs, except for the taxa *Fagus* and *Quercus*. We can, therefore, summarise the differences between designs for the remaining taxa by describing the pollen assemblages of WP2 and CW2. The differences between CW2 and WP2 were not pronounced for the taxa Cichorioideae (0.1 – 0.3%), *Plantago* (0.2 – 0.8%), *Pinus* (3.5 – 3.1%) and *Abies* (0.2%). For *Betula* and *Fraxinus* the differences were moderate, in the order of 4-5%. Larger differences occur for *Corylus* and *Poaceae*. Their proportions in CW2 were about 10%, whereas in WP2 they were 21-22%.

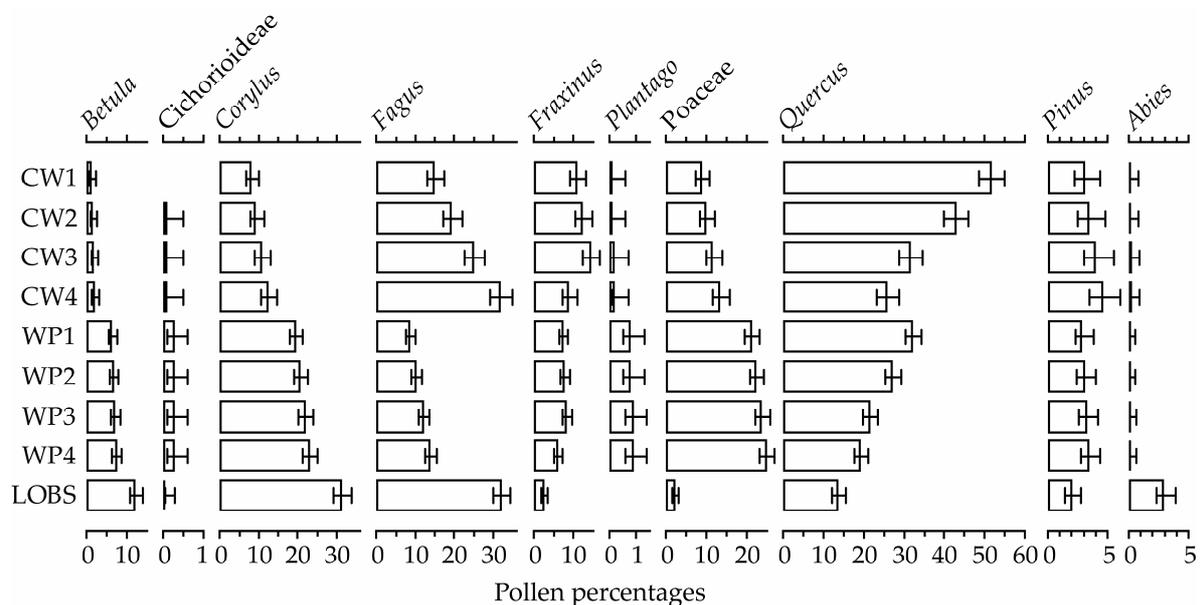


Figure 3 Simulated pollen assemblages for closed wood (CW) and wood pasture (WP) scenarios as well as the observed pollen assemblage of Lobsigensee at 6000 cal. years BP (LOBS). The error bars depict the 95% confidence intervals of the pollen percentages

In Figure 3, the simulated results are compared to the observed mean pollen assemblage from Lobsigensee. The observed *Fagus* content was rather high (34%). Such a high *Fagus* pollen percentage resulted only from the CW4 scenario (31%). The best matching *Quercus* percentage resulted from scenario WP4 (19% versus 23% observed). For *Betula* and *Corylus* the WP4 results were closest to the observed proportions (12 and 32%, respectively). The observed *Fraxinus* proportion (3%) was closest to WP4 (6%). The observed proportion of all NAP was 2.4%. The simulated proportions of herbaceous taxa were higher, ranging between 9 and 14% for CW1 to 4 and between 22 to 26% for WP1 to 4. Considering the sum of herbaceous taxa, the CW1 to 4 matched best with the observed pollen data.

Discussion and conclusion

In this study, we created two landscape designs based on the closed canopy and the wood pasture hypothesis. The level of landscape openness that we designed in our simulations cannot provide the causes of the openness directly. We can only indicate whether the simulated pollen assemblages reflect the trends found in an observed pollen assemblage in a lake of similar size.

Some aspects of the simulated pollen assemblages were similar to Lobsigensee assemblage. Firstly, the low NAP at Lobsigensee being closest to CW1 were in favour of the closed wood design; all herbaceous taxa had significantly higher relative abundances in the wood pasture simulations. Secondly, *Fagus* as the dominant taxon in the Lobsigensee pollen record, was better approximated by the closed wood landscape designs, and the observed value was similar to that in CW4. However, there are also some points in favour of the wood pasture designs: the pollen percentages of *Betula*, *Corylus*, *Fraxinus*, and *Quercus* were closer to the results of the wood pasture scenario. The proportions of the two remaining taxa, *Pinus* and *Abies*, were only simulated in shoreline (for pine only) and regional vegetation, and therefore not very indicative to any design.

Although the regional vegetation composition was similar for all simulations, the effect of the composition on the simulated pollen assemblages was different, because of the different size of the RSAP. While the RSAP was smaller for the “closed wood”, the background component will theoretically be larger here thus causing the somewhat higher *Pinus* proportions in CW1 to 4. The RSAP were a little larger than found for modern sites at the Swiss Plateau, but in other regions also larger RSAP in the same order of size (out to 1700 m) have been found (Nielsen, 2004; Nielsen and Sugita, 2005).

The high *Fagus* content in the Lobsigensee pollen assemblage and the observed low NAP point to an extended vegetation cover of woodland dominated by beech (e.g., CW4). Also, we can deduce that *Quercus* vegetation cover was not very abundant within such woodland (less than 5%, see Table 2). On the other hand, the *Corylus* proportion of Lobsigensee was quite high. Assuming the PPE of *Corylus* to be correct (Soepboer *et al.*, in press), and knowing that the *Corylus* vegetation proportion we used for the shrub-phase was, in fact, overestimated because we lack PPE for thorny bush taxa, the reason for this underestimation of *Corylus* in the pollen assemblage is likely to be found in the landscape designs. This may indicate

that the area of shrub-phase cover was underestimated in the wood pasture design and that the shrub-phase was wrongfully left out of the closed wood design. In addition, the regional *Corylus* component may have been higher. Given the regional setting around Lobsigensee with a meandering Aare river and extensive wetland areas of the Grosse Moos, the amount of open habitats (either naturally or through frequent disturbances) may present enough forest fringes for hazel to colonize. It is also conceivable that the vegetation was more influenced by factors such as flooding, nutrient-poor soils, wind-throw, and animal browsing than was anticipated in the closed wood theory, a suggestion put forward by several authors (Svenning, 2002; Bradshaw *et al.*, 2003; Mitchell, 2005).

There are different ways to design landscapes for simulation purposes. Landscape designs of higher complexity, e.g. randomized landscapes (Bunting, pers. com.), might be more appropriate to test vegetation theory. For instance, we did not design any landscapes with a high *Corylus* and a high *Fagus* cover, because our primary aim was to assess the two opposites in forest theory with our simple model approach. Nevertheless, the experiment described in this study provides insights into the complexity of estimating vegetation openness in the past.

A different option is to quantitatively reconstruct past vegetation using the “Landscape Reconstruction Algorithm” (Sugita, 2007a, b). This approach enables estimating vegetation proportions at regional and local scale in regions where PPE and pollen data from multiple lakes of various sizes are available. The reconstruction of regional vegetation in Sweden has shown that the landscape openness around 6000 cal. BP was not larger than 10-20% (Sugita *et al.*, 2007). Yet, openness might be better indicated at a local scale (Fyfe, 2007). Although the LRA approach will give vegetation cover estimates, the distribution of the taxa over the landscape remains to be assessed.

It is also possible to spatially define vegetation structures based on, for instance, elevation, slope, and soil moisture to create a ‘real-world’ past landscape design (e.g., Fyfe, 2006). A similar approach (Vervoort, 2006) in which past vegetation on the Swiss Plateau was simulated with a land use change model (Verburg *et al.*, 2002) suggested that RSAP could be estimated, however, that detailed biophysical information is necessary to estimate pollen assemblages. There, the spatial resolution (100 m) of for instance the elevation data seemed too large to accurately simulate past pollen counts for the investigated lakes (Vervoort, 2006).

Different landscape designs and vegetation compositions might produce similar results, or even results that are more similar to the Lobsigensee values. Based on the results of this simple simulation experiment we conclude that the mid-Holocene pollen assemblages observed at Lobsigensee and at many other Swiss Plateau sites are likely the result of vegetation cover that consisted of rather closed beech forests. The high *Corylus* proportion in the observed pollen assemblage shows that the disturbance area must have been larger than can be expected from the closed forest theory alone. On the other hand, our results indicate that the extent of openness as suggested by Vera (2000) and Kirby (2004) is too high. Natural (e.g. river plains, wetlands, poor soils) and disturbance-induced (floods, wind-throw, fire) relatively small openings in closed beech forests may have produced the observed pollen assem-

blage at Lobsigensee 6000 years ago. Still, palynology can never exactly give the reason why open patches or open landscapes occurred, and thus other data and modelling approaches should also be explored further (see also Bradshaw *et al.*, 2003).

CHAPTER 5

MODELLING REGIONAL VEGETATION CHANGES ON THE SWISS PLATEAU DURING THE PAST TWO MILLENNIA

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Abstract

We estimated present-day and past regional vegetation abundance on the Swiss Plateau using a modelling approach (REVEALS) and pollen assemblages from large lakes (≥ 520 ha). The modern regional vegetation composition estimated by REVEALS compared well to the present-day landscape. A regional vegetation composition over the past 2000 years was reconstructed in 200-year intervals using pollen assemblages from three large lakes. The REVEALS results showed a much higher anthropogenic impact on vegetation throughout the past 2000 years than the pollen percentage diagrams would suggest. The reconstructed vegetation changes reflected the differences in agricultural and other human activities in the region during the Roman Time, the Migration Period, the early and late Middle Ages, and the onset of Modern Times. With the exception of the Migration Period, cereals covered most of the Swiss Plateau during the past two millennia.

Introduction

Quantitative reconstruction of vegetation cover has long been called for by various disciplines concerned with global environmental change, forest ecology, or archaeology. In the absence of remote sensing data or written documents, pollen records retrieved from natural archives such as lake and mire deposits, have traditionally been used to describe vegetation changes in the past. However, fossil pollen assemblages are the end-product of the complex interactions that take place in a sedimentary basin and its surrounding landscape (Prentice, 1988). Moreover, reconstructions of past vegetation and their interpretation have often been largely intuitive rather than quantitative (Davis, 2000).

Developments of theoretical models and concepts have dramatically improved our understanding of the pollen-vegetation relationship over the past two decades (Prentice, 1985, 1988; Sugita, 1993, 1994). Recently, (Sugita, 2007a, b) developed a new framework of vegetation and landscape reconstruction across various spatial and temporal scales, the Landscape Reconstruction Algorithm (LRA), based on these theoretical and conceptual developments. The LRA uses a linear relationship between pollen loading and the surrounding vegetation as the fundamental model for vegetation reconstruction (Prentice, 1985; Sugita, 1994). The linear pollen-vegetation relationship consists of two components: taxon-specific pollen productivity (the slope of the linear pollen-vegetation relationship) and background pollen (the y-axis intercept of the linear relationship). Such pollen-vegetation relationships have been observed empirically and tested for several regions of North America and Europe (Calcote, 1995; Sugita *et al.*, 1999; Broström *et al.*, 2004; Nielsen, 2004; Bunting *et al.*, 2005; Soepboer *et al.*, 2007).

Despite recent advances in the study of pollen-vegetation relationships, quantitative reconstruction of past vegetation has been hampered by a lack of knowledge concerning the changes in background pollen through time. Sugita (2007a; 2007b) first recognised the usability of scale for the reconstruction of past vegetation. It has been long known amongst pollen analysts that basin size affects the composition of a pollen assemblage (Tauber, 1967; Berglund, 1973; Janssen, 1973; Jacobson and Bradshaw, 1981): with increasing lake size, the influence of local vegetation decreases in favour of pollen originating from regional vegetation. This implies that pollen assemblages from large sites are similar within a region and represent mainly regional vegetation, while pollen assemblages from smaller basins consist of a local as well as of a regional pollen component. Changes in pollen assemblages of large lakes are, therefore, able to provide information about changes in the background pollen in small lakes.

The LRA consists of two sub-models, REVEALS and LOVE, each suitable for a different spatial scale. REVEALS (Regional Estimates of VEgetation Abundance at Large Sites) allows to quantitatively reconstruct regional vegetation composition within a 100-400 km radius from pollen records collected from large lakes, equal or larger than 100 ha (Sugita, 2007a). LOVE (LOcal VEgetation Estimates) allows estimating local vegetation abundance by using regional vegetation estimates from REVEALS and pollen assemblages from small to medium-sized lakes (Sugita, 2007b).

In this study, we test REVEALS using modern pollen assemblages from large lakes (≥ 520 ha) on the Swiss Plateau by comparing the averaged model results to the observed composition of vegetation and land cover classes in the region. Then, we use REVEALS to reconstruct regional vegetation for the past two millennia quantitatively using fossil pollen records from several sites in the region to assess changes in land use and landscape openness.

Methods and materials

REVEALS

The REVEALS model (Sugita 2007a) is expressed as,

$$\hat{V}_i = \frac{n_{i,k} / \hat{\alpha}_i K_i}{\sum_{j=1}^m (n_{j,k} / \hat{\alpha}_j K_j)} \quad (1),$$

where \hat{V}_i : estimate of regional vegetation composition for species i [%],

$n_{i,k}$: pollen count of species i at site k ,

$\hat{\alpha}_i$: estimate of pollen productivity (PPE) for species i , relative to a reference taxon,

t : number of plant taxa used for reconstruction, and

K_i : the “pollen dispersal-deposition coefficient” of species i , defined as $\int_R^{Z_{\max}} g_i(z) \cdot dz$.

In the definition of K_i , R represents radius of a large lake [m] from which pollen samples are collected, Z_{\max} a radius from within which >90% of pollen comes from [m] (i.e., the spatial extent of the “regional” vegetation), z is the distance from a point at the centre of the lake [m], and $g_i(z)$ a pollen dispersal-deposition function for species i . For this study, the Sugita model (1993) of pollen dispersal and deposition on the entire surface of a basin, which is appropriate for lakes, is used as $g_i(z)$.

REVEALS estimates vegetation composition in percentages in a given region, and long-distance pollen coming from beyond the region, defined by Z_{\max} (see definition above). For this study, Z_{\max} is set to 200 km from each lake. Assuming a homogeneous vegetation Sugita (1993) showed that >90% of all taxa used in this study comes from 200 km. Conceptually, REVEALS is similar to the R-value model (Davis, 1963), but can be considered as a more general model. The R-value model does not incorporate the bias caused by the inter-taxon differences in pollen dispersal and deposition. When the pollen dispersal-deposition coefficient, K_i , is set to 1.0 for all taxa, REVEALS is the same as Davis’ (1963) R-value model. Pollen dispersal and deposition is taxon-specific, however. It is thus critical to include the pollen dispersal-deposition coefficient for quantitative reconstruction of the regional vegetation composition (Sugita, 2007a).

Parameter estimates and model settings

Pollen productivity estimates (PPE, $\hat{\alpha}_i$ in eq. 1) were recalculated for this study using ERV sub-model 3 as implemented in the software *erv.v6.2.varcov* (Sugita, unpublished, Sugita 2007a, b). The input data was the same as in Soepboer *et al.* (2007), namely surface sediment

pollen assemblages sampled at 20 small lakes on the Swiss Plateau and the surrounding vegetation abundance of these lakes. However, vegetation increment sizes for the Ring-Source model (Sugita *et al.*, 1999) was 200 m in contrast to 10 m as in Soepboer *et al.* (2007). The ERV model also provides the variance and covariance of PPE among plant taxa, required to calculate the standard errors for the estimates of regional vegetation abundance (Sugita 2007a). The PPE for Cerealia was set to 0.1.

PPE obtained by Soepboer *et al.* (2007) and the adjusted Cerealia PPE have been successfully validated by simulating pollen counts for an independent set of eleven small to medium-sized lakes on the Swiss Plateau and comparing them to the observed pollen counts (Soepboer *et al.*, in press). In order to calculate the pollen dispersal-deposition coefficient, several parameters included in Sugita's (1993) model are set to the same values as those in Sugita (2007a) and Hellman *et al.* (2007). Fall speed of pollen in air, another critical parameter for pollen dispersal and deposition, is listed in Table 1.

Modern and fossil pollen records

In this study we used pollen records from four large lakes on the Swiss Plateau (Figure 1). The Baldeggersee (47°10'N, 8°17'E, 463 m above sea level (asl), water surface area 520 ha) pollen data is a composite of two cores taken in the deepest part of the basin at 66 m of water depth: for the period between 1993 and 1885 we used an annually laminated freeze-core (Lotter *et al.*, 1997b; van der Knaap *et al.*, 2000), whereas for the period before 1800 AD a 863 cm long Kullenberg core sampled for pollen at 20 cm intervals was used (Giger *et al.*, 1984).

A 100 cm long gravity core taken in 1999 at a water depth of 48 m in the deepest part of Hallwilersee (47°17'N, 8°12'E, 449 m asl, water surface area 990 ha) was dated by varve counts back to 1920 AD (Lotter, unpubl. data), and a constant accumulation rate was assumed for the older sediment. Pollen samples were analysed every centimetre (van Leeuwen, unpubl. data).

Table 1 Pollen productivity estimates (PPE, derived from ERV sub-model 3), their standard deviation, pollen fall speed per taxon, and the present-day land cover based regional vegetation estimate (LCV)

taxon	PPE	st.dev. PPE	fall speed (m s ⁻¹)	LCV (%)
Poaceae	1.00	0.00	0.035	19.2
<i>Abies alba</i>	9.26	2.91	0.12	3.8
<i>Betula</i> spp.	2.68	0.23	0.026	1.9
<i>Carpinus betulus</i>	4.84	1.83	0.042	0.5
Cerealia (sum)	0.10	0.17	0.078	22.2
Compositae SF Cich.	0.16	0.03	0.051	5.5
<i>Corylus avellana</i>	2.26	0.20	0.025	2.0
<i>Fagus sylvatica</i>	0.83	0.20	0.055	13.5
<i>Fraxinus excelsior</i>	1.46	0.13	0.022	4.6
<i>Picea abies</i>	0.59	0.18	0.056	20.7
<i>Pinus (cembra & sylvestris)</i>	0.71	0.35	0.041	1.2
<i>Plantago lanceolata</i>	0.40	0.12	0.029	1.2
<i>Quercus</i> spp.	2.59	0.28	0.035	3.8

Greifensee (47°20'N, 8°40'E, 435 m asl, water surface area 850 ha) was cored in 1976 with a Kullenberg corer and analyzed for pollen in 10 cm intervals (Wick, 1988). For Zugersee (47°6'N 8°29'E, 413 m asl, surface area 38.3 km²) the Kullenberg core ZG-17 collected in 1973 at a water depth of 195 m (Kelts, 1978) was used. This core was sampled in 20 cm intervals for pollen analysis (Ammann, 1979).

The age-depth relationship for each lake was established by various methods. When radiocarbon dates or varve counts were not available, we correlated the palynological records with well-dated pollen diagrams from the Swiss Plateau (Ammann *et al.*, 1996). The following distinct features in the palynostratigraphy were used as key dating points: the first occurrences of *Juglans*, *Castanea*, and *Secale* in connection with a peak in *Quercus* pollen percentages (Ammann, 1989) were used as indicators for the Roman colonization of the Swiss Plateau and dated to 2000 years BP (1 AD). A post-Roman peak in *Fagus* pollen percentages together with a small peak in *Fraxinus* (Ammann, 1989) was dated to 1450 years BP (500 AD). The onset of a phase with *Cannabis* pollen (Ammann, 1989) was dated to 850 years BP (1100 AD). The year of coring was used as age of the sediment surface. Linear interpolation between these dating points was used to attribute ages to the different pollen samples.

TILIA (Grimm, 1992), a graphing and data-analysis program for palynological data, was used to produce averaged pollen counts in equally-spaced time intervals of 200 years to allow a better comparison of the major changes in landscape development among sites for comparable time-windows.

First, present-day vegetation derived from land cover data was compared to a mean vegetation composition as estimated by REVEALS, derived from surface sediment pollen samples from Baldeggersee (two sample average, 1991-1992) and Hallwilersee (two sample average, 1989-1993).

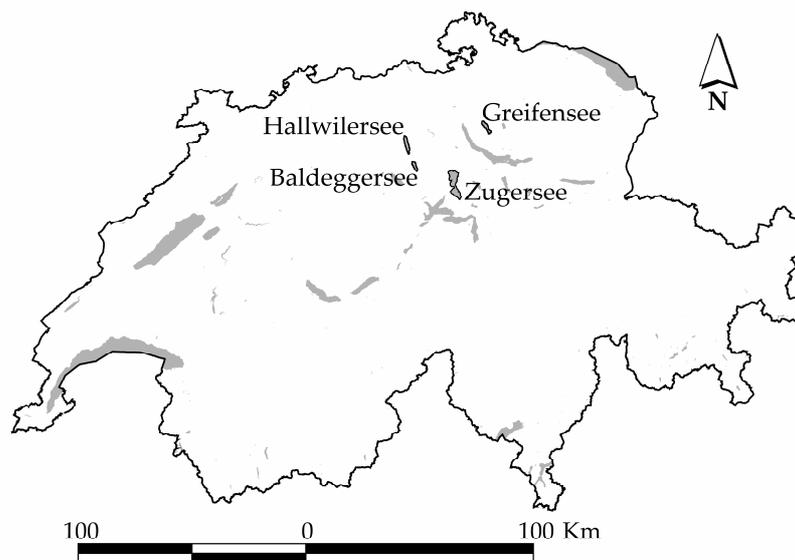


Figure 1 Map of Switzerland with location of large Swiss lakes used in this study. Grey areas represent large water areas

Table 2 The level of detail used for determining the present-day regional vegetation estimate based on CORINE land cover. 'Area' shows the distribution of the land cover classes within the 200 km-region on and around the Swiss Plateau. 'Total 13 taxa' sums up the proportion that the 13 taxa represent within the vegetation composition

Code	Class	Area (%)	Total 13 taxa (%)
100	Artificial surfaces	5.5	0
200	Agricultural areas (except arable land and pastures)	9.4	0
210	Arable land	15.9	75
230	Pastures	13.1	56
311	Deciduous forests	12.2	83
312	Coniferous forests	12.7	92
313	Mixed forests	9.6	77
320	Scrub and/or herbaceous vegetation associations	10.0	51
330	Open spaces with little or no vegetation	9.5	0
410	Wetlands	0.2	82
510	Water bodies	1.9	0

Next, vegetation was estimated using REVEALS based on the averaged 200 year-pollen assemblages of Baldeggersee, Hallwilersee, and Greifensee. We assumed the mean output of these three lakes to represent the regional vegetation changes on the Swiss Plateau. Because the Hallwilersee pollen record covers only the past 400 years, a larger part of reconstruction was based on the reconstruction of Baldeggersee and Greifensee only.

In comparison to the other sites, Zugersee is located at the border of the Alps with the effect that the regional vegetation might be biased by the subalpine vegetation belt. The vegetation estimated by REVEALS using Zugersee pollen data is, therefore, analysed separately to assess how its location closer to the Alps is affecting the predicted vegetation. Still, we used this reconstruction for comparison with the central Swiss Plateau sites.

Modern land cover

We defined the region from where to expect 90% of the pollen to be 200 km around the Swiss Plateau, thus comprising large parts of Switzerland, parts of southern Germany, France, northern Italy, Austria, and Liechtenstein (see also Soepboer *et al.*, in press). For the regions outside Switzerland the CORINE (Coordination of information on the environment) land cover map compiled by the European Union was used, based on remote sensing images from 1999-2001. The land cover classes have three integrated levels of detail, of which the most detailed level contains 44 classes (EEA, 2005). The spatial resolution is 100 m. The division into 11 classes used in this study (see Table 2) results from combining certain land cover classes.

For the Swiss area we used a Swiss land use map from 1992-1997 that is reclassified by the Swiss Federal Statistic Office to correspond to the CORINE classification by the European Union (GEOSTAT, 1998). This map contains 13 classes, of which one contains all forested areas combined. As we wanted to use a division into mixed, deciduous, and coniferous forests corresponding to the CORINE land cover database of the other countries, the Swiss land cover map was overlain with a 100 m resolution forest cover (GEOSTAT, 1992) to allow a better level of detail. Then, the land cover maps from Switzerland and the other areas were

combined (Soepboer *et al.*, in press). The distribution of the 11 land cover classes within the 200 km region on and around the Swiss Plateau is listed in Table 2.

Species composition within land cover classes was mostly based on field surveys on the Swiss Plateau (Soepboer *et al.*, 2007), whereas the percentage of cereals in the arable land was estimated from Swiss land-use statistics (SFSO/AGR, 2000). Next, the regional land cover composition was estimated using the combined CORINE land cover database and the vegetation composition. The resulting land cover-based vegetation abundance estimates (LCV) for the 13 pollen taxa PPE are available for on the Swiss Plateau sum up to 54% of the total vegetation cover. In the modelling, it is assumed that no other species are present; therefore, the percentages were recalculated to make the sum of 13 taxa equal to 100% (Table 1).

Results

Present-day vegetation

In Figure 2 a mean pollen assemblage of Baldeggersee and Hallwilersee, a present-day REVEALS vegetation reconstruction, and LCV are shown. According to the LCV, in the present-day vegetation cover Cerealia had the highest proportion (22%), followed by *Picea* (21%), Poaceae (19%), and *Fagus* (13%).

In the averaged surface sediment pollen assemblage, taxa like *Fagus*, *Plantago lanceolata*, and Poaceae compared well with the LCV. However, Figure 2 shows that the sum of herbaceous taxa (including Cerealia) were underrepresented in the pollen assemblage. The averaged pollen record indicated hardly any Cerealia, whereas they accounted for more than 20% in the present-day vegetation cover.

The REVEALS vegetation estimates were closer to the LCV for *Abies*, *Betula*, *Carpinus*, Cerealia, Comp. SF. Cichorioideae, *Corylus*, *Fraxinus*, *Picea*, and *Quercus*. Compared to the LCV, REVEALS produced higher discrepancies for Poaceae (underestimated by 12%) than was found in the mean pollen assemblage (overestimated by 2%). On the other hand, the sum of herbaceous taxa (Cerealia, Poaceae, *Plantago lanceolata*, and Compositae SF Cichorioideae) of the REVEALS vegetation estimate was remarkably similar to the LCV.

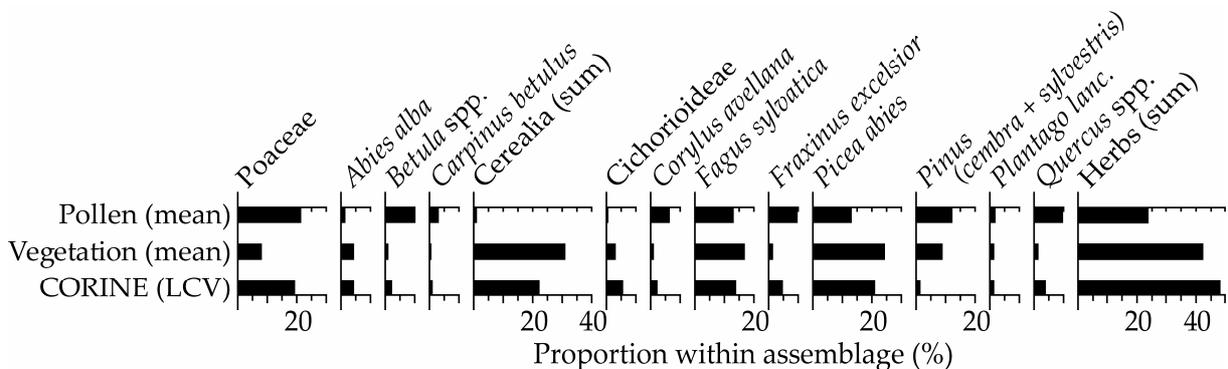


Figure 2 Comparison of pollen percentages (mean of surface sediment samples from Baldeggersee and Hallwilersee), vegetation estimates by REVEALS (mean vegetation estimates based on pollen data from Baldeggersee and Hallwilersee), and CORINE vegetation estimates

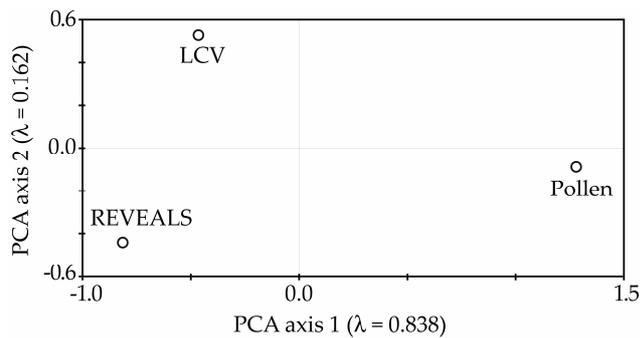


Figure 3 Principal Component Analysis of pollen percentage data, CORINE land cover-based vegetation (LCV) and regional vegetation estimate by REVEALS, showing the first two PCA axes. The PCA was performed with a log transformation of the data

of herbs, in which *Cerealia* was most abundant (33%). During the following period (200-400 AD) the cover of trees and shrubs increased. Half of the vegetation cover (48%) consisted of *Fagus*.

After 400 AD, openness increased and the influence of *Fagus* diminished. The highest values for the total of herbaceous taxa were found between 1000 and 1800 AD, e.g., *Cerealia* reached a cover of 78%. After 1800 AD some reforestation occurred, most notably by coniferous species. *Cerealia* cover decreased to 55%.

Figure 5 depicts the regional vegetation abundance derived from the Zugersee pollen record for the past 2000 years. Also in this REVEALS reconstruction the degree of openness is high. For the period 1-200 AD, the herb cover amounts up to 30%. However, more reforestation phases are found than in Figure 4. Also *Abies* is more abundant than *Fagus*, in contrast to the central Swiss Plateau sites. Between 200-800 AD and 1200-1600 AD *Abies* cover increased with values of 45 and 40%, respectively.

The regional vegetation estimates by REVEALS are summarised in Figure 6, and compared to mean pollen assemblages. Here, *Pinus*, *Picea* and *Abies* are combined into 'coniferous', *Quercus*, *Corylus*, *Fagus*, *Fraxinus*, *Betula*, and *Carpinus* into 'deciduous', and Poaceae, *Cerealia*, Cichorioideae and *Plantago lanceolata* into 'herbs'. Clearly, in the pollen diagrams the NAP is much smaller, whereas the proportion of deciduous taxa is much higher compared to the REVEALS-based vegetation reconstruction.

In Figure 3, a principal component analysis (PCA) of the REVEALS reconstruction together with averaged surface sediment pollen data and the LCV shows that the REVEALS estimates were closer to the LCV than the mean pollen assemblage.

Reconstruction of past vegetation

The REVEALS reconstruction of past vegetation composition on the Swiss Plateau (Figure 4) indicates that the landscape in the past two millennia was far more open than could be inferred from a percentage pollen diagram. The earliest time period studied (1-200 AD) showed already 40% vegetation cover

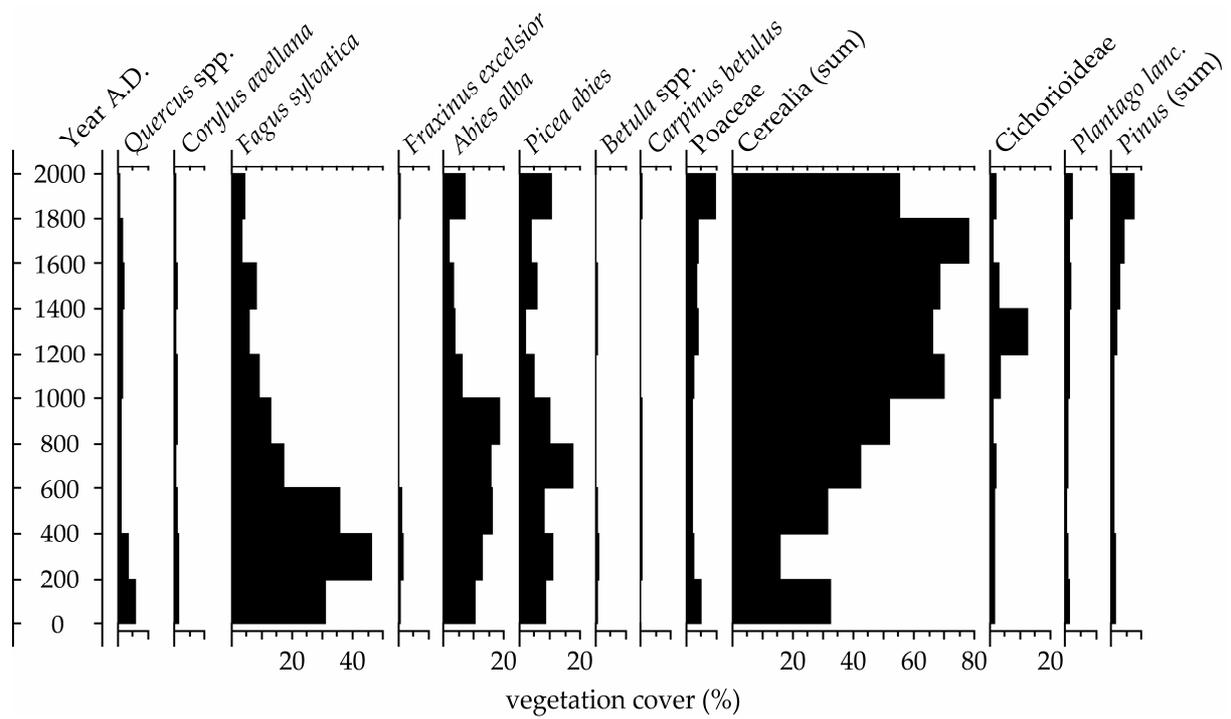


Figure 4 REVEALS modelled regional vegetation cover for the Swiss Plateau over the past 2000 years

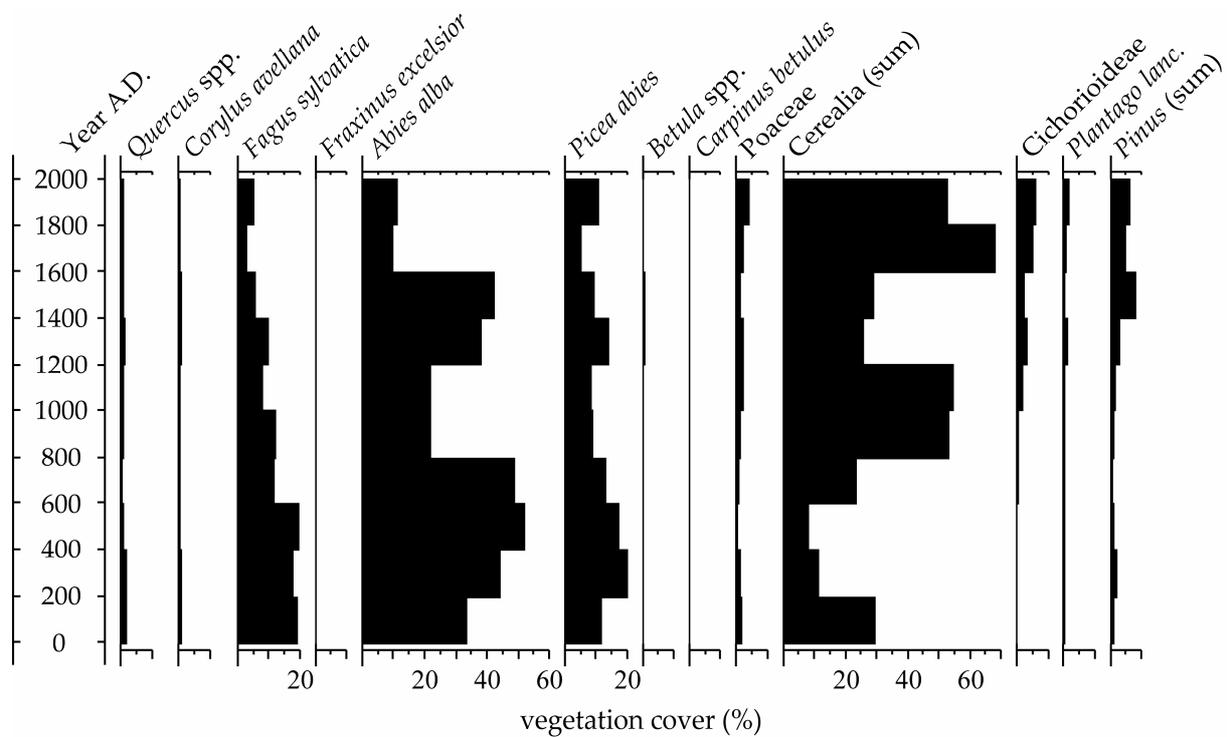


Figure 5 REVEALS modelled vegetation cover from Zugersee pollen data

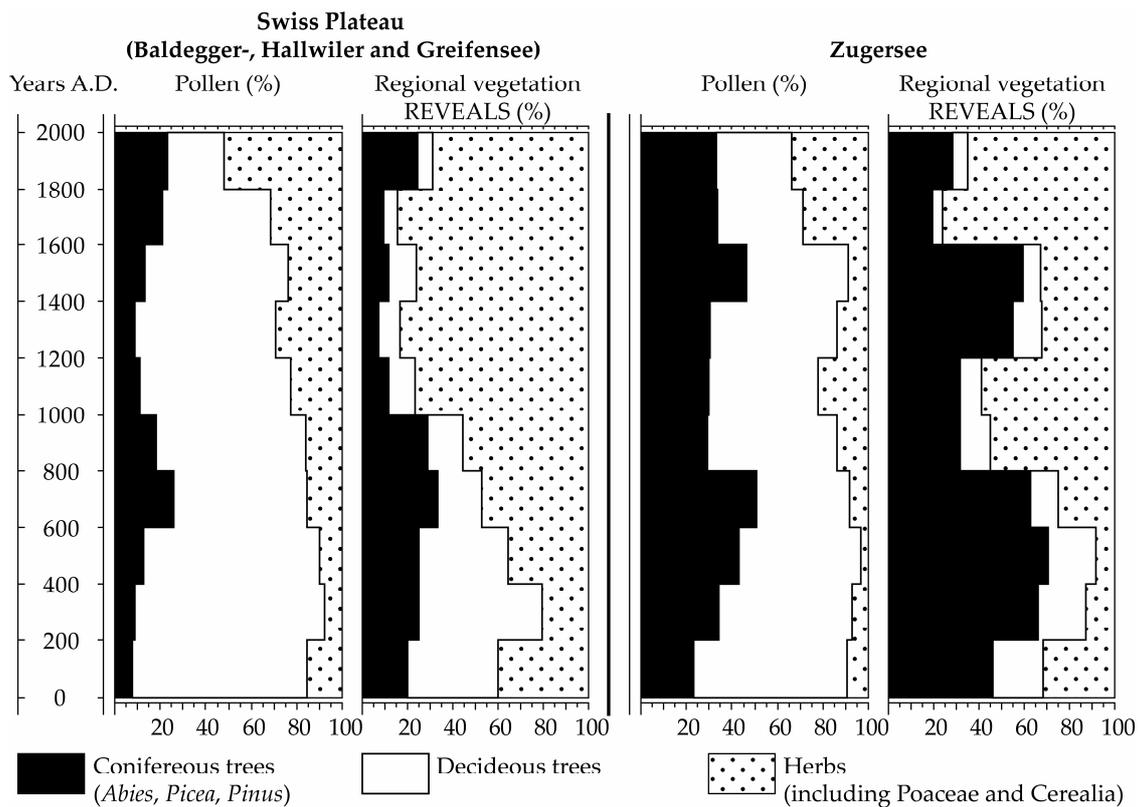


Figure 6 Summary pollen-percentage diagram and summary diagram of reconstructed regional vegetation abundance on the Swiss Plateau and on the edge of the Swiss Plateau (Zugensee)

Discussion

The program for REVEALS include subroutines to estimate standard errors for the estimates of regional vegetation abundance. The standard errors on the vegetation estimates presented here are very high and are sometimes larger than the estimated values. These large error estimations are caused by the low number of sites used in the REVEALS reconstruction. A higher number of sites would be preferable in reconstruction past vegetation. However, Sugita (2007a) showed that the average estimates of multiple sites will remain the same, even though a low number of sites is used. Therefore, we can assume that the averaged results of even a low number of sites are reflecting regional changes. The comparison of the present-day mean pollen assemblage, the REVEALS reconstruction, and the LCV for the same time period (Figure 2 and 3) indicated that the REVEALS reconstruction was more comparable to the LCV than the mean pollen assemblage. This conclusion corroborates Swedish field studies by Hellman *et al.* (2007).

In this study, the reconstruction was limited to 13 taxa for which PPE were available. These taxa were, on one hand, initially chosen because they are prominently represented in the pollen assemblages from small lakes. On the other hand, they are indicators for specific land cover classes (Soepboer *et al.*, 2007). However, in the present-day regional vegetation composition derived from the CORINE land cover these 13 taxa sum up to 54% of all present plant species. This low number is chiefly caused by the exclusion of agricultural land cover other

than cereals and grassland. Also, species that are important in the present-day vegetation, such as *Trifolium pratense* and *T. repens*, are sparsely present in pollen assemblages, because they are not wind-pollinated. Another reason for not including species is the fact that fall speed measurements are either not available or that pollen grain characteristics prevent the calculation of pollen fall speed. Finally, the regional PPE dataset as elaborated by Soepboer *et al.* (2007) is limited because of statistical restrictions; for the models the number of taxa should (preferably) not exceed half the number of sites.

PPE

We applied PPE that were derived from present-day data from small to medium-sized lakes on the Swiss Plateau. By using these as a first approximation (Sugita, 2007a) to reconstruct past vegetation on the Swiss Plateau, we are assuming that PPE have not changed through time. However, this assumption may not be realistic as the present-day PPE for different regions clearly differ already. Although sampling strategies (e.g. moss polsters versus lake surface sediments and differences in vegetation surveys) may partly explain these differences (Broström, 2002; Soepboer *et al.*, 2007), pollen productivity may also differ between regions because of factors such as climate, competition, or different vegetation age, size and genotypes, geology, soil types, or vegetation cover density (e.g., Calcote, 1995). However, the 200-year averaged pollen samples smooth out small year to year variation in pollen productivity due to climate, such as described by Sjögren *et al.* (2006). Still we cannot entirely rule out effects on pollen productivity of, for instance, the Little Ice Age. However, a modelling approach as used here will enable the evaluation of PPE variability when needed (Sugita *et al.*, 2007).

Regional vegetation history

During the entire studied time frame unforested areas, including agricultural land, have been present on the Swiss Plateau. While in late Holocene lake sediments from the Swiss Plateau herb pollen values were rarely over 30% (see Figure 6), REVEALS-based vegetation estimates suggested the unforested area extended up to 80%. This confirms reconstructions for Sweden that also have indicated larger openness in vegetation for the past 3000 years (Sugita *et al.*, 2007).

The earliest period that was studied here is the Roman Time (50 BC to 400 AD, (e.g., Burga and Perret, 1998). The 1-200 AD reconstruction corresponds to this period. The anthropogenic influence on the vegetation is high during this time, while we find an unforested cover of 40%, including Cerealia proportions of 33%. In our reconstruction, *Fagus* was the dominant tree on the Swiss Plateau, whereas at Zugersee *Abies* played a more prominent role.

The reconstruction of 200-400 AD showed signs of a forest recovery phase, with *Fagus* (and *Abies* at Zugersee) being the dominant species and unforested areas decreasing to 20% cover. This phase is likely to reflect (the onset of) the Migration Period (400-500 AD, e.g., Rösch *et al.*, 1992) during and after the collapse of the Roman empire. The results might also indicate population decrease caused by pandemics (Rösch *et al.*, 1992), thus reducing the human impact on the vegetation cover.

The 600-800 AD reconstruction is characteristic of the Early Middle Ages (Tinner *et al.*, 2003). Until the 12th century AD, the common land use system was a biannual field-grassland rotation system (Rösch *et al.*, 1992). According to our results, cereal cultivation increased during the Early Middle Ages. The so-called wood pastures (Bürgi, 1999) have not led to high vegetation estimates of *Quercus* in the Middle Ages: highest *Quercus* values are found in the Roman Time (6%) and 1600-1800 AD (2%). Between 600 and 800 AD the Swiss Plateau forests were dominated by *Fagus*, while *Abies* and *Picea* were more abundant at higher altitudinal belts.

Cerealia estimates increase fast from 800-1000 AD onwards, whereas hardly any tree exceeds 10%. Between 1200 and 1800 AD, the Cerealia vegetation estimate stays over 60%. This finding confirms the description by Rösch *et al.* (1992) that favourable climatic conditions, new technologies (e.g. for ploughing) and the introduction of a three-field rotation system (summer wheat - winter wheat - fallow) in the 12th and 13th century caused an economic drive, population increase, and intensification of land use.

We don't find a clearly defined effect of the impact of wars, pandemics (Black Death), and climatic deterioration (Abel, 1978 in Rösch *et al.*, 1992) in the Late Medieval Period (~1250 to 1500 AD). Rösch (1998) suggested that because of the decreasing population, agriculture on the heavier, more difficult to till, soils was abandoned. We might see the effect of these events in the stabilisation of Cereal-production starting 1200 AD. There is a slight decrease in modelled vegetation proportions of Cerealia in the period between 1400 and 1600 AD. However, the differences are not much pronounced.

Cerealia vegetation estimates of 1600-1800 AD periods indicate a last large expansion of Cerealia cultivation to values of up to 80%. In the 1800-2000 AD reconstructions the proportion of Cerealia decreased significantly, at the same time an increase of most other taxa takes place, particularly Poaceae and *Picea*. These changes might be explained by artificial fertilisation, new harvesting methods, the intensification of agriculture, and the introduction of *Zea mays*. Also, since 1900 the fields were not left fallow anymore (Karg, 1995).

According to Bürgi (1999) the pattern of forested and open landscape on the Swiss Plateau did not change much since the Middle Ages, because of wood supply from the pre-Alps and Alps. However, the use of forest has changed through time. While in the early 1800s most forests were still primarily used for traditional uses such as the collection of firewood, the growing need for commercial timber caused coppice woods to decline since the mid-19th century (Bürgi, 1999). The increase in *Picea* and *Pinus* in the vegetation reconstructions of the youngest period is likely a reflection of the increase in commercial timber production. However, due to the 200-year averaged time steps some of the larger changes in land use that were visible at a higher resolution, are now levelled out in the 1800-2000 AD reconstruction.

Reconstructing the scale of Cereal cultivation

The vegetation reconstructions clearly showed a much higher proportion of cereals in the landscape than would intuitively be expected from the original pollen assemblages. Even though, based on the modern land cover comparison an overestimation of about 8% may be

expected, the amount of cereal cultivation seems to have been high throughout the past two millennia.

Besides the possibility of an overestimation, there are some other uncertainties in the Cerealia reconstructions. First of all, due to their low abundance in the pollen records and the fact that their pollen is not always distinguishable to species level, the different cereal pollen types (Cerealia undiff. and *Secale*) were combined into one Cerealia taxon for modelling purposes. However, combining the different Cerealia pollen types has some drawbacks. Firstly, the different cereal species have different pollen dispersal properties. For instance, the pollen of *Secale cereale* is more easily dispersed. Because we used an average pollen fall speed for the Cerealia type, based on the pollen grain characteristics of *Secale cereale*, *Triticum aestivum*, *Hordeum vulgare*, and *Avena sativa*, the effects of different dispersal of Cerealia species through time were somewhat smoothed out. Secondly, during the past 2000 years the preference for certain crop types has changed (Rösch *et al.*, 1992), changing the composition within the Cerealia sum.

The PPE for Cerealia used here was not calculated by an ERV-model because the original PPE was found to be so low that this would influence the reconstruction dramatically. The original value may have originated from the discrepancy between surface pollen assemblages and vegetation caused by the lack of information in the vegetation survey and vegetation composition on different rotational schemes of crops.

Moreover, the Cerealia pollen-vegetation relationship may have changed over time. For instance, pollen dispersal may have been influenced by different agricultural methods over time. Crop weeds identified in archaeobotanical findings pointed to different agricultural methodologies in different times (Rösch, 1998). For instance, the Romans used large-scale agriculture with fertilisation. The Early Medieval period showed high species diversity with many weeds, indicating a return to small-scale agriculture. Towards the High Medieval period long-cultivated soils deteriorated and less favourable soils were turned into arable land (Rösch, 1998). Furthermore, different harvesting methods over time may also have caused differences in pollen dispersal (Nielsen and Odgaard, 2004).

Despite these issues, it is necessary to include Cerealia in the pollen assemblage when modelling the past 2000 years of land cover change. As a cultivated crop, changes in Cerealia cover are directly influenced by human decisions. When 'raw' pollen percentage would have been used to reconstruct past land cover, up to 20% of cereal cover could have been ignored. Such an underestimation of the openness of a landscape will also influence estimates with regard to regional climate, hydrology, or surface albedo.

Conclusions

When using a present-day dataset, REVEALS vegetation estimates were more comparable to LCV than the pollen assemblages (%). Especially the Cerealia estimate was closer to the LCV. The sum of herbaceous taxa was comparable between the LCV and the REVEALS reconstruction, thus justifying the use of REVEALS for land cover reconstruction.

The regional vegetation compositions in 200 year-averaged time intervals as estimated by REVEALS showed a much higher anthropogenic impact and openness of the landscape than could be concluded from pollen percentages alone. Both the sum of herbaceous taxa and the reconstructed *Cerealia* vegetation cover demonstrated this. We could attribute inferred vegetation developments to historical periods of the past two millennia: the Roman Time, the Migration Period, the Early Middle Ages, and the onset of Modern Times. With the exception of the Migration Period, our results suggest that cereals were the dominant taxon on the Swiss Plateau during the past two millennia.

ALGEMENE INLEIDING EN SAMENVATTING

(SUMMARY IN DUTCH)

Inleiding

Modelleren van landoppervlakbedekkingen in het verleden gaat over de biofysische eigenschappen van het oppervlak van de aarde en de directe onderlaag. Bossen, graslanden en moerassen zijn voorbeelden van landoppervlakbedekking. De landbedekking wordt tegenwoordig voornamelijk beïnvloed door het landgebruik, bijvoorbeeld het beheren van productiebos, het fokken van vee, en het bedrijven van landbouw. De landoppervlakbedekking en het landgebruik worden beïnvloed door klimatologische, biofysische, en sociaaleconomische factoren (Turner II *et al.*, 1995). Daarentegen worden klimaatveranderingen beïnvloed door veranderingen in bodemvochtigheid, verdamping, en albedo (Fuller en Ottke, 2002). Albedo is de hoeveelheid zonnestraling die door het aardoppervlak wordt weerkaatst. Al deze biofysische factoren zijn weer direct verbonden met landoppervlakbedekking.

Inmiddels voltrekken zich ecologische veranderingen zoals verwoestijning, afname van zoetwater, verlies van biodiversiteit en opwarming van het mondiale klimaat. De oorzaken en gevolgen van de klimaatopwarming zijn nog niet helemaal bekend. Wel heeft Ruddiman (2003, 2006) een theorie voorgelegd dat de invloed van de mens op het klimaat al met de ontdekking van de landbouw (8000 jaar geleden) is begonnen. Het is daarmee belangrijk geworden om het aardesysteem in het verleden te bestuderen. Het begrip van het systeem én de kennis van het verleden geven informatie over de huidige stand van zaken en over te verwachten toekomstige mondiale omgevingsveranderingen. De complexiteit van het systeem vraagt ook het begrip van landoppervlakbedekking- en landgebruiksveranderingen in het verleden.

De veranderingen van landoppervlakbedekking in het verleden worden bij gebrek aan geschreven documenten of satellietbeelden gevonden door stuifmeelmonsters te analyseren. Al in 1916 realiseerde Von Post dat de analyse van fossiel stuifmeel uit veen- of meerkernen de vegetatiesamenstelling kon weergeven uit de tijd dat het stuifmeel werd afgezet, als een soort satellietbeeld van die tijd (Prentice, 1988). In elk groeiseizoen registreert het bemonsterde bassin (bijvoorbeeld een meer, moeras of moskussen) de hoeveelheid stuifmeel die door de omringende vegetatie wordt vrijgegeven. De verschillende plantensoorten geven vaak ook verschillende soorten stuifmeelkorrels. Het analyseren van het stuifmeel uit de se-

dimentkernen staat het bestuderen van vegetatieverandering over tijdperioden van 10^1 tot 10^6 jaar toe (zie Berglund *et al.*, 1996; Birks, 2005).

Maar het verband tussen stuifmeel en vegetatie is wel gecompliceerd. Het stuifmeel kan op verschillende manieren van de plant in het afzettingsbassin terecht komen (zie Prentice, 1988). Verschillen tussen het stuifmeelassemblage in het bassin en de daadwerkelijke vegetatiesamenstelling kunnen zijn veroorzaakt door de verschillende stuifmeelproductiviteit van plantensoorten, en de verschillende verspreiding en conservatie van stuifmeelkorrels (Prentice, 1988; Jackson, 1994). Bovendien is het vaak, ondanks continue ontwikkelingen in de palynologie (Punt *et al.*, 2003; Beug, 2004), moeilijk of soms onmogelijk om stuifmeel tot op soort of zelfs geslacht (Prentice, 1988) te identificeren. Vegetatiepatronen spelen ook een rol. De planten dicht bij een afzettingsbassin zullen daarin meer stuifmeel afzetten dan planten verder weg. Ook zal de bassingrootte de samenstelling van een stuifmeelmonster beïnvloeden: in grotere bassins is de invloed van regionale vegetatie groter dan van lokale vegetatie (Andersen, 1970; Janssen, 1973; Jacobson en Bradshaw, 1981; Prentice, 1988; Sugita, 1994). De stuifmeelproductiviteit van een soort kan ook nog regionaal verschillen (Calcote, 1995).

Het internationale POLLEN-LANDscape CALibration netwerk (POLLANDCAL; het kalibreren van stuifmeel en landschap) is een internationaal netwerk van wetenschappers die (onder andere) proberen methoden te ontwikkelen om kwantitatieve vegetatie/landschapskenmerken op diverse ruimtelijke schalen vast te stellen. Dit wordt gedaan voor de bescherming van omgevingskwaliteiten en landschapsbeheer op lokale schaal en ook voor omgevingsonderzoek op regionale tot mondiale schaal.

Dit proefschrift is een bijdrage aan het POLLANDCAL netwerk. Het specifieke doel van dit proefschrift is om beter inzicht te krijgen in de resultaten van stuifmeelanalyses. Dit wordt gedaan door de verhouding tussen moderne stuifmeelafzettingen en de omringende vegetatie te analyseren. En deze vervolgens te gebruiken voor het testen van hypothesen en het reconstrueren van regionale vegetatie in het verleden. Het onderzoek werd uitgevoerd met stuifmeel- en vegetatiegegevens van het Zwitsers Plateau. Hier zijn de productiefste gronden van Zwitserland te vinden en is het reliëf golvend tot heuvelachtig. Ook liggen daar veel meren waarin in lange tijdperioden stuifmeel is gesedimenteerd

Overzicht van de hoofdstukken

Schattingen van stuifmeelproductie op het Zwitsers Plateau om landoppervlakbedekking kwantitatief te kunnen reconstrueren

Een eerste doel van deze studie was het bepalen van stuifmeelproductiviteitschattingen (Pollen Productivity Estimates; PPE) voor kruid- en boomsoorten op het Zwitserse Plateau en het bijbehorende relevante brongebied voor stuifmeel (Relevant Source Area of Pollen; RSAP). Daarom werden de moderne vegetatie en de stuifmeelafzetting vergeleken voor 20 kleine tot middelgrote meren en hun invloedsgebied. De vegetatie rond de meren werd onderzocht in luchtfoto's en in het veld. De stuifmeelgegevens uit de oppervlaktesedimenten waren al eerder geanalyseerd en werden gebruikt om de huidige stuifmeeldepositie in deze meren te geven.

Dertien plantensoorten zijn uiteindelijk uitgekozen, voornamelijk gebaseerd op hun voorkomen in het stuifmeel. Enkele uitgezochte stuifmeeltaxa kwamen niet veel voor in het stuifmeel, maar wel in de vegetatie. Sommige hadden een indicatorwaarde voor verschillende types van landoppervlakbedekking. Sommige taxa die indicatief zijn voor azonale (natte) vegetatie zoals *Salix*, *Alnus* of *Populus* werden uitgesloten. De gekozen taxa waren: *Alba abies* (zilverspar), *Corylus avellana* (hazelaar), *Carpinus betulus* (haagbeuk), Compositae onderfamilie Cichorioideae (composietenfamilie), *Plantago lanceolata* (smalle weegbree), *Fagus sylvatica* (beuk), *Fraxinus excelsior* (es), *Betula* (berk), *Quercus* (eik), *Picea abies* (spar) en Poaceae (grassen). *Pinus cembra* en *P. sylvestris*-type werden gecombineerd tot *Pinus* (den) en het Cerealia-type en *Secale cereale* tot Cerealia (tarwe, haver, gerst, rogge). De Poaceae werden gebruikt als referentietaxon, d.w.z., de PPE van Poaceae werd gelijkgesteld aan 1.

De PPE werden geschat met verschillende methoden. Eén soort methoden heeft betrekking op het kalibreren van de stuifmeel-vegetatie verhouding (Extended R-value (ERV) model, met drie submodellen). De andere methode heeft betrekking op hoe stuifmeelverspreiding gemodelleerd kan worden. Hierbij kunnen verschillende manieren worden gebruikt om een gewicht aan de afstand van de vegetatie tot de meeroevers toe te kennen. Het Prentice-Sugita model gebruikt hiervoor onder andere valsnelheid van het stuifmeel en snelheid van de wind. De overige methoden gebruiken alleen afstand als parameter.

De RSAP bleek het gebied te zijn tot 800 m vanaf de meeroevers, ongeacht de toegepaste wegingsmethode of het ERV-submodel. De PPE van de meeste boomsoorten waren hoger of gelijk aan 1. Alle kruidtaxa hadden PPE lager dan 1, maar de PPE voor Cerealia waren lager dan 0,1. De resultaten tussen de drie ERV-submodellen verschilden lichtjes. De verschillende afstandwegende benaderingen beïnvloedden de PPE voor *Abies* veel meer dan die voor andere taxa. Het taxonspecifieke Prentice-Sugita model zal vermoedelijk de beste PPE van *Abies* geven, omdat dat model meeneemt dat de stuifmeelkorrel van *Abies* veel zwaarder is dan die van andere taxa.

Een vergelijk tussen PPE van het Zwitsers Plateau en andere regio's in Europa gaf aan dat de PPE tussen regio's in Europa kunnen verschillen. Zelfs wanneer de bemonsteringsstrategieën voor vegetatie en stuifmeel worden gestandaardiseerd, kan de stuifmeelproductiviteit nog door bijvoorbeeld klimaat, vegetatiestructuur, geologie en bodem worden beïnvloed. Bovendien kunnen regionale verschillen voorkomen op soort- of geslachtsniveau van de plant.

Het evalueren van Zwitserse PPE door simulatietechnieken

De PPE voor het Zwitserse Plateau werden geëvalueerd omdat ze soms afweken van andere PPE die in Europa gevonden waren. De stuifmeelassenblages voor elf Zwitserse meren werden gesimuleerd met behulp van het programma POLSIM. POLSIM maakt ook gebruik van ERV-submodellen, maar berekent de pollenassenblages als de PPE en vegetatie bekend zijn. De elf meren waren niet gebruikt om de PPE te berekenen. De lokale vegetatie werd berekend in een gebied tot 5 km vanaf de oevers van de meren. Hiervoor werd een landoppervlakbedekkingskaart op redelijk grote schaal (100 m resolutie) gebruikt, opgedeeld in 12 landoppervlakbedekkingsklassen. Drie verschillende PPE werden gebruikt, namelijk diegene eerder waren berekend door de drie ERV-submodellen. Deze PPE waren verder verkregen

door gebruikt te maken van het Prentice-Sugita model en een constante windsnelheid van 3 m s^{-1} . Voor Cerealia werd een aangepaste PPE-waarde gebruikt, omdat de originele waarde statistisch te laag was om te worden gebruikt. De regionale vegetatie werd op twee manieren geschat. De eerste manier maakte gebruik van landbedekkingsgegevens in een gebied van 200 km op en rond het Zwitserse Plateau. De tweede manier gebruikte de gemiddelde gegevens van de eerder genoemde landoppervlakbedekking tot aan 5 km vanaf de oevers van de bestudeerde meren. POLSIM simuleerde vervolgens de stuifmeelassenblages. Deze werden vergeleken met de geanalyseerde stuifmeelassenblages uit dezelfde meren.

Wanneer de regionale vegetatieschatting gebaseerd op de gegevens van de landbedekking tot 200 km werd gebruikt, week de meerderheid van de gesimuleerde stuifmeelpercentages maximaal 5% af. Veelal was ook het dominante taxon correct geschat. De resultaten die mede gebaseerd waren op een regionale landoppervlakbedekking tot 5 km vanaf de meren, waren minder nauwkeurig.

De resultaten van het onderzoek wijzen erop dat PPE die voor het Zwitserse Plateau werden gevonden (met inbegrip van de aangepaste PPE voor Cerealia), kunnen worden gebruikt om met een redelijke nauwkeurigheid stuifmeelassenblages te simuleren. Zij kunnen daarom ook voor andere doelstellingen worden gebruikt, zoals het reconstrueren van vegetatie in het verleden. Dat het gebruik van een gedetailleerde regionale vegetatieschatting de simulaties verbeterde, toont het belang van een nauwkeurige regionale vegetatieschatting. De resultaten toonden ook aan dat de gebruikte modellen ook in landschappen kunnen worden toegepast met een relatief complex reliëf.

Het schatten van vegetatieopenheid in het verleden met behulp van stuifmeel-vegetatie verhoudingen: een modelbenadering

Als PPE en RSAP voor een regio beschikbaar zijn, kunnen hypothesen over vegetatieopenheid in het verleden getest worden. Hiertoe werden twee eenvoudige scenario's voor een mid-holoceen landschap (ca. 6000 jaar geleden) in laagland Zwitserland ontworpen. Het eerste bestond uit open parkachtig bos, waarin de vegetatiefasen door de aanwezigheid van grote herbivoren worden bepaald. Het tweede scenario bestond uit bos met een grotendeels gesloten bladerdak en kleine openingen waar regeneratie plaats kan vinden. Daarna werd POLSIM gebruikt met de landschapsscenario's voor het verleden simulaties uit te voeren om stuifmeelgegevens te verkrijgen. De gesimuleerde stuifmeelassenblages werden vergeleken met een typisch mid-holoceen stuifmeelassenblage (uit Lobsigensee).

Het lijkt erop dat het landschapontwerp gebaseerd op bos met een gesloten bladerdak de grootste overeenkomst had met het waargenomen mid-holocene stuifmeelassenblage. Toch bevatten alle gesimuleerde stuifmeelassenblages hogere waarden van Poaceae en *Quercus* en lagere waarden van *Abies*, *Corylus* en *Betula*. Het hoge aandeel *Corylus* in het waargenomen stuifmeelassenblage toont aan dat het verstoringsgebied groter moet geweest zijn dan in een dicht bos kan worden verwacht. Natuurlijke (bv., riviervlaktes, moerasland, slechte bodems) en door verstoringen (overstromingen, windslag, brand) veroorzaakte openingetjes in beukenbos met een gesloten bladerdak kunnen het waargenomen stuifmeelassenblage in Lobsigensee 6000 jaar geleden hebben geproduceerd.

Het modelleren van regionale vegetatieveranderingen op het Zwitserse Plateau tijdens de afgelopen twee millennia

De beschikbare PPE staan ook het schatten van regionale vegetatiehoeveelheden voor verschillende perioden op het Zwitserse Plateau toe, namelijk met een modelbenadering waarbij stuifmeelassenblages van grote meren worden ingezet (>100 ha). Hiervoor wordt het model REVEALS gebruikt. REVEALS is een submodel van het Landschap Reconstructie Algoritme. Een tweede submodel, LOVE, schat de vegetatiepercentages op lokale schaal, mede gebaseerd op de resultaten van REVEALS.

Als eerste werd een vergelijking gedaan met resultaten van REVEALS, gemiddelde stuifmeelgegevens en daadwerkelijke vegetatie voor de huidige tijd. Het huidig vegetatievoorkomen was geschat via landoppervlakbedekkingsgegevens. De gemiddelde schatting door REVEALS (gebaseerd op stuifmeelgegevens uit twee grote meren op het Zwitsers Plateau) was over het algemeen en vooral voor Cerealia en het totaalpercentage van de kruidige soorten, nauwkeuriger dan het gemiddelde van de waargenomen stuifmeelassenblages.

Vervolgens werd een regionale vegetatiesamenstelling gereconstrueerd voor perioden van 200 jaar tot 2000 jaar geleden. Hierbij werden stuifmeelassenblages uit drie grote meren gebruikt. De resultaten van REVEALS geven aan dat een veel hoger antropogeen effect op de vegetatie heeft plaatsgevonden in de afgelopen 2000 jaar dan vermoed werd uit de stuifmeelanalyses alleen. De aangetoonde vegetatieveranderingen wezen op verschillen in landbouwmethoden en andere menselijke activiteiten in het gebied tijdens de Romeinse Tijd, de Volksverhuizingperiode, de vroege en late Middeleeuwen, en het begin van Moderne Tijd. Met uitzondering van de Volksverhuizingperiode werd het landoppervlak van het Zwitserse Plateau tijdens de afgelopen twee millennia voor het grootste deel bedekt door graansoorten.

Conclusies

In dit proefschrift werden Zwitserse PPE voor 13 pollentaxa geïntroduceerd, geëvalueerd, gebruikt voor het testen van vegetatiehypothesen en de reconstructie van vegetatie in het verleden. De reeks methoden was tot nu toe nog niet toegepast op een glooiend tot heuvelachtig landschap zoals het Zwitsers Plateau. De resultaten in Hoofdstukken 3 en 5 waarbij simulaties voor de huidige tijd worden vergeleken met waarnemingen leveren bewijs dat de Prentice-Sugita modellen ook voor zulke topografische complexere landschappen kunnen worden gebruikt. Voor de bepaling van PPE worden traditioneel stuifmeelassenblages uit kleine openingen in het bos of moskussentjes gebruikt (Calcote, 1995; Broström *et al.*, 2004). Uit hoofdstuk 3 blijkt dat, hoewel de foutenmarges groter kunnen zijn, de PPE die uit kleine tot middelgrote meren wordt afgeleid ook betrouwbaar kunnen zijn.

Deze PPE kunnen voor grote meren worden gebruikt om veranderingen van landoppervlakbedekking in het verleden te reconstrueren. In Hoofdstuk 5 werd een regionale vegetatiereconstructie gemaakt voor de afgelopen 2000 jaar. De reconstructie toonde aan dat de openheid van het regionale landschap veel hoger was dan verwacht uit de stuifmeelassenblages alleen. De resultaten geven de noodzaak aan om bij het interpreteren van stuifmeelgegevens het landschap te bekijken vanuit “stuifmeelperspectief” (bijvoorbeeld met het Prentice-Sugita

model). Met de regionale vegetatiereconstructie is het nu ook mogelijk om lokale vegetatie voor dezelfde tijdsperiode te reconstrueren.

In Hoofdstuk 4 werd een simulatiebenadering gebruikt om twee tegenstrijdige theorieën over de schaal en de oorzaken van openheid in natuurlijke bossen te vergelijken. Uit de resultaten blijkt dat POLSIM inderdaad als hulpmiddel kan dienen om alternatieve hypothesen te testen. Wel is er nog ruimte voor het uitbreiden van deze simulatiemodellen. Het onlangs ontwikkelde hulpmiddel LRA opent een breed scala van onderzoektoepassingen naar de oorsprong en de schaal van landschapsopenheid in het verleden en het invloed hiervan op het aardesysteem.

Vooruitzicht

Het beschikbaar komen van Zwitserse PPE staan het verdere testen van openheid en vegetatiepatronen op het Zwitserse Plateau in het verleden toe. Wanneer meer meren worden onderzocht, kunnen de PPE van meer taxa worden berekend en zo de modellering van landoppervlakbedekking in het verleden worden uitgebreid. De recente ontwikkeling van LOVE staat de schatting van lokale vegetatie in een gebied van circa 1 km rondom kleine meren op het Zwitserse Plateau toe. Deze schaal is van belang voor archeologen en natuurbeheerders.

Het beschreven onderzoek geeft aan dat het landschap in de afgelopen twee millennia vermoedelijk opener was dan eerder gedacht. Het menselijke effect op het landschap was dus vermoedelijk ook groter dan gedacht. Deze openheid heeft ook wezenlijke invloeden op biofysische factoren, zoals op de albedo van het aardoppervlak en de bodemvochtigheid, en zou daarom ook in klimaatmodellen moeten worden opgenomen. Wanneer de regionale vegetatie op een gedetailleerdere tijdschaal en over langere tijdsperiodes wordt geschat, komt meer informatie beschikbaar over de interactie tussen landoppervlakbedekking en klimaatverandering. Daarnaast kan de vergelijking tussen landoppervlakbedekking, erosiesnelheden, en overstromingsfrequenties in het verleden beleidsmakers inzicht geven hoe de huidige situatie verschilt van die in het verleden. Misschien kan een verandering van landoppervlakbedekking helpen om de huidige kwesties op het Zwitserse Plateau op een duurzame manier op te lossen.

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CURRICULUM VITAE

Welmoed Soepboer was born in Leeuwarden on June 8th, 1977. She completed secondary school (VWO) at the Stedelijk Gymnasium in Leeuwarden in 1995 and started her study “Soil, Water and Atmosphere” at Wageningen University. She chose “Soil Science”, later on specialising in “Soil Inventarisation and Land Evaluation” and “Remote Sensing”. In a first thesis, she described the relationship between climate factors and vegetation parameters derived from satellite imagery in the Sahel and Europe. A second thesis concerned the modelling of future land use change at the island Sibuyan in the Philippines. During her studies, she spent six months at the department of Chemical Agriculture and Soil Science at the University of Sydney, Australia. She graduated in 2001, at the same time completing the MSc “Geo-information Science”. From April 2002 to June 2006 she worked at the department of Palaeoecology, Utrecht University, on the PhD research described in this thesis. For this thesis she spent two months of 2004 in St. Paul, USA, at the University of Minnesota. The remainder of 2006, she worked as a project leader archaeological pre-research. Currently, she works as a consultant engineer (environmental impact assessment).



At Anna Broström's PhD defence party in Lund, Sweden, 2002

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